

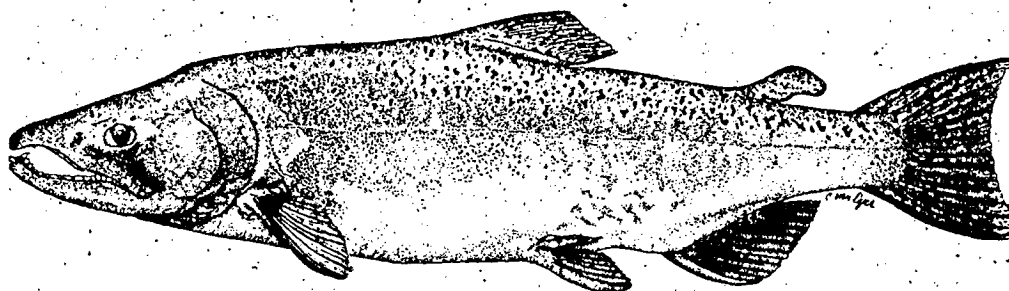
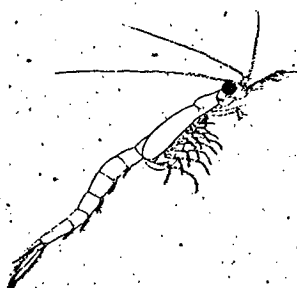
STATUS AND TRENDS REPORT

ON

AQUATIC RESOURCES

IN THE

SAN FRANCISCO ESTUARY



 *San Francisco Estuary Project*



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STATUS AND TRENDS REPORT ON
AQUATIC RESOURCES
IN THE SAN FRANCISCO ESTUARY
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PREFACE

In recognition of the special need to protect the water quality and natural resources of our nation's estuaries, Congress passed the Water Quality Act of 1987. This act amended the Clean Water Act and established the National Estuary Program. The Program, administered by the U.S. Environmental Protection Agency, requires the development of Comprehensive Conservation and Management Plans (CCMP) for the nation's most significant estuaries.

As enabled by the Water Quality Act, the Governor of California nominated the San Francisco Bay/ Sacramento-San Joaquin Delta for inclusion into the National Estuary Program. In response, the Administrator of EPA formally established the San Francisco Estuary Project (the Project) in April 1988. The Project is a planning effort with broad-based involvement of the public and local, state and federal agencies. The Project's goals adopted by its participants are:

1. Develop a comprehensive understanding of environmental and public health values attributable to the Bay and Delta and how these values interact with social and economic factors.
2. Achieve effective, united and ongoing management of the Bay and Delta.
3. Develop a Comprehensive, Conservation and Management plan to restore and maintain the chemical, physical and biological integrity of the Bay and Delta, including restoration and maintenance of water quality, a balanced indigenous population of shellfish, fish and wildlife, and recreation activities in the Bay and Delta, and assure that the beneficial uses of the Bay and Delta are protected.
4. Recommend priority corrective actions and compliance schedules addressing point and non-point sources of pollution. These recommendations will include short and long-term components based on the best scientific information available.

Under authority of the Water Quality Act, the Project has five years in which to convene a Management Conference, identify and characterize the Estuary's priority problems, and develop a CCMP. The Project is scheduled to complete the CCMP by November 1992. After adoption by the Management Conference, the CCMP must be approved by the Governor of California and the Administrator of the EPA. Once approved, the Plan will guide local, state and federal agencies in efforts to improve protection of the Estuary.

The Project's Management Conference, with over 100 participants representing environmental, business and government interests has identified five management issues of concern;

- 1) Decline of Biological Resources,
- 2) Increased Pollutants,
- 3) Freshwater Diversion and Altered Flow Regime,
- 4) Increased Waterway Modification, and
- 5) Intensified Land Use.

To characterize and better define the management issues, the Project is preparing a series of Status and Trends Reports (STRs). These technical reports seek to develop a scientific consensus on the major aspects of the issues and identify important gaps in information and knowledge. In this characterization phase of the Project, individual Project subcommittees oversee the development of these reports. STRs have been prepared on: 1) Dredging and Waterway Modification, 2) Wetlands and Other Habitats, 3) Land Use and Population, 4) Pollutants, 5) Aquatic Resources, and 6) Wildlife.

In addition, SFEP is preparing several other reports during the characterization phase including: a report on land use regulation and the impact of land use change on the future environmental health of the Estuary; a report on freshwater flows to estimate the effect that flow variability has on selected biological parameters; a report on the entrapment zone to evaluate the freshwater needs of various aquatic species; a report on quality assurance and quality control procedures to examine opportunities for enhanced sampling techniques and laboratory analysis; and a report evaluating the regulatory and management programs responsible for managing the Estuary's resources.

The characterization effort will culminate in the completion of a "State of the Estuary" report. This report will summarize the information in the individual technical reports and provide an objective assessment of current conditions in the Estuary. This assessment will set the stage for developing the CCMP with its attendant management recommendations.

This STR on Aquatic Resources reviews the status and trends of bacterial, plant, invertebrate, and piscine resources within the Estuary and their relationships with each other and with physical parameters. It is the product of more than two years of effort by members of SFEP's Biological Resources Subcommittee, as well as staff at SFEP. This edition of the STR was preceded by three earlier drafts which received many written and verbal comments representing a wide range of viewpoints.

The role of the Biological Resources Subcommittee deserves further explanation. The Subcommittee was formulated to represent a cross-section of SFEP participants. The Subcommittee consisted primarily of environmentalists and government agency representatives, and also included the participation of representatives from the regulated community. The Subcommittee provided oversight of the consultants, who prepared the Status and Trends Report. This consisted of reviewing drafts, writing comments and providing verbal comments during Subcommittee meetings. In conjunction with the review of this document, the Subcommittee members, particularly Perry Herrgessel of the California Department of Fish and Game spent many hours preparing on their own, a set of Goals and Management Options to address critical protection issues in the San Francisco Estuary. Using this approach, SFEP will be able to develop a CCMP that is responsive to the findings of this report, the Project participants and the public.

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Status and Trends Report for Aquatic Resources

EXECUTIVE SUMMARY

I. Introduction

The Sacramento-San Joaquin Estuary encompasses a diverse set of interconnected habitats and supports a large and diverse array of aquatic resources. These aquatic resources have high economic and aesthetic value to the people of California. The geography and climate of California have led to evolutionary adaptations by many native species that allow them to thrive under the naturally fluctuating conditions. However, alterations of the Estuary and its water supplies by humans have resulted in habitats increasingly unsuitable for native aquatic organisms. In addition, alterations of the environment have paved the way for the invasion of many species introduced from Asia and eastern North America. The biological needs of these species, both native and introduced, continue to conflict with human use of the Estuary's land and water. The purpose of this report is to document present status and long-term trends in the populations of aquatic organisms in the Estuary. The report consists of two main parts:

- 1) A description of the distribution, relative abundances, and trends through time of various animal species that inhabit the Estuary.
- 2) A general description of the amount of food (carbon/energy) available to animal species and the various pathways by which this food enters and leaves the food web of the Estuary (Appendix A).

II. Distribution, Relative Abundances, and Trends through Time

A. Causes of Change

Three factors predominate in controlling the distribution and abundance of most animals of San Francisco Bay and Delta:

1. Climatic changes, both in oceanic conditions (such as *El Niño* events and upwelling) and continental conditions (principally variability in rain and snowfall).
2. Physical features of the estuary, such as basin morphology, salinity, and temperature. The distance a habitat is from the ocean or from fresh water strongly affects its salinity, temperature, and water movements that, in turn, strongly control which species it supports.
3. Human activities over the last 130 years. These activities can be grouped into four categories:

- a. Introduction of non-native species. Hundreds of species have been introduced into the estuary, both intentionally and unintentionally. Many of these species have thrived, some producing major economic benefits (e.g. striped bass), others creating

ecological problems (e.g. the clam *Potamocorbula amurensis*), and many with minor or unknown effects.

b. Pollution. Early sewage disposal into the Bay eliminated some species from affected areas. Improved sewage treatment has allowed substantial recovery in those areas. Industrial pollutants and urban runoff, particularly organic chemicals, heavy metals, and thermal pollution, are now the main concerns in the Bay. Agricultural chemicals and other nonurban runoff are more important in the Delta.

c. Modification of waterways and wetlands. As with pollution, the pace of alteration has slowed in recent years, with even permits for port dredging becoming difficult to obtain because of possible effects on aquatic resources. During the Gold Rush era unintentional filling of riverbeds due to hydraulic mining in the Sierra led to flooding and the effects of the massive quantities of silt delivered to the estuary may still be affecting water quality. Other dramatic alterations include: transformation of large areas of tidal wetlands into evaporating ponds in San Francisco Bay; construction of Bayfarm and Treasure Islands from dredging spoils; and dredging and diking of the Delta to create farmland.

d. Modification of regime of freshwater inflow and outflow. These modifications today are predominantly diversions required for operation of the State Water Project and the Central Valley Project. During recent dry years these diversions, together with many smaller agricultural diversions within the Delta, have taken more than half of the potential inflow of the Estuary. The resulting reductions in outflow have many effects on aquatic species, including amplification of the effects of drought, change in direction of net flow in several main channels of the Delta, increased entrainment in diversions, and changes in food webs.

B. Trends in Major Groups of Organisms

Primary producers. Bacteria, protozoans, algae, and macrophytes in the Estuary provide much of the carbon that is the basis of the food webs. Long-term trends in the populations of these organisms are poorly understood, but major changes have and are taking place, with repercussions through the food web. Recent examples of changes have been (1) aperiodic blooms of the diatom *Melosira granulata* in the Delta, a species which seems to be hard for most zooplankton grazers to feed upon and (2) recent reductions in the abundance of phytoplankton in Suisun Bay, apparently as the result of intensive filtering by large populations of an introduced clam.

Zooplankton. Zooplankton populations are sampled regularly only in the Delta and Suisun Bay, so it is not possible to say much about trends in other parts of the Estuary. Even for the Delta and Suisun Bay, abundance information exists only from 1972. The smallest zooplankters, rotifers, have declined sharply throughout the Delta, and populations have been very low since 1979. Trends are less evident in Suisun Bay, but rotifer populations

in general are smaller now than they were in the 1970s. **Cladocerans** (water fleas), an important food source for small fish, have also shown a long-term decline in abundance. However, the decline in cladocerans was more sudden than that of rotifers and occurred mainly in the late 1970s after rotifer populations had already declined. **Copepods** have more complex trends. Most freshwater species show declines like those of the cladocerans, while marine species (mainly *Acartia tonsa*) show no trends except a crash in response to the clam invasion. The estuarine copepod *Eurytemora affinis*, important as food for shrimp and larval fish, has shown a long-term decline, but it has been at least partially replaced by three introduced species of copepods. The introduced species are apparently less suitable as prey, however. The abundance of **opossum shrimp** (*Neomysis mercedis*) is closely tied to that of *E. affinis* and to freshwater flow into the Bay, but any long-term trends are obscured by large fluctuations in numbers.

Benthos. Most of the benthic organisms in the Estuary are introduced species, and most have little information available on their population trends. In different parts of the Estuary, the dominant benthic species depend in large part on the recent history of freshwater outflow from the Delta and saltwater intrusion. Populations of **oysters and marine clams** have fluctuated largely in response to harvest, pollution, and invasions of new species, that displace resident species, but there seem to be no real long-term trends. Reduction of organic pollution in recent years has made Bay molluscs safer to eat, so a fairly substantial sport fishery for them has developed. The recent explosive invasion of the Asian clam (*Potamocorbula amurensis*) may result in declines of other benthic organisms. The **Dungeness crab** is the most studied member of the Bay benthos because of its valuable fishery. However, its abundance is controlled mainly by oceanic conditions outside the Bay, so the low numbers of crabs landed in San Francisco since the 1960s probably are not related to Bay conditions. Four species of **grass shrimp** are harvested in the Estuary, but only the species tied most closely to freshwater inflow, *Crangon franciscorum*, seems to show a long-term decline in abundance. The abundance of other species is more tied to marine events. **Crayfish** are harvested in the Delta in abundance, but long-term trends have not been investigated.

Chinook salmon. Four major runs of chinook salmon pass through the Estuary during their migrations as adults and juveniles. All four runs have shown severe and continuing declines in numbers in the past century and are maintained in large part by hatchery production. The winter run chinook is listed as a threatened species. While the primary causes of the declines are dams and diversions upstream of the Estuary, in recent years it has been demonstrated that passage through the Delta is a major source of mortality, especially when outflows are low and export pumping rates are high.

Striped bass. Striped bass, although an introduced species, have become symbolic of conditions of the Estuary as their fishery has shown a long, continuous decline and they are the best studied species in the system. Their numbers are now (1991) at a record low. Many factors may have contributed to this decline including toxic contamination, inadequate

food supplies, reduced egg production of females, and overfishing (including poaching), but the overwhelming factor has been water diversions, especially from the Delta.

Sturgeon. Of the two species in the Estuary, less is known about the green sturgeon, but it appears to be in a decline worldwide. White sturgeon abundance is tied to its spawning success in years of very high outflow and to the rate at which it is exploited. Although the data are scanty, these factors together may have led to a population decline in recent years.

Planktivorous fishes. Small fishes that feed on zooplankton are among the most abundant in the estuary, and their population trends reflect conditions in different parts of the estuary. **Northern anchovy** are by far the most numerous fish in the San Francisco and San Pablo bays. They show large fluctuations in numbers in response to both marine and estuarine conditions, but there are no obvious population trends in recent years. **Pacific herring** move into the Bay in large numbers for spawning. From 1974 until recently, there has been an increasing trend in spawning stock abundance, but the reasons for these trends are not known. Short-term changes in abundance were noted during the *El Nino* conditions of 1983. **American shad** are an abundant anadromous species about which surprisingly little is known in the Estuary. They spawn least successfully in dry years, presumably due to a combination of stressful conditions for young shad and increased entrainment, so it is not surprising that their numbers have declined during the recent drought period. **Delta smelt** have shown a major decline in abundance in the past 10 years, to the point where they may be on their way to extinction. This species is endemic to the upper estuary and has a 1-year life cycle, so it seems to be especially vulnerable to the combination of increased diversions from the Delta and drought. **Longfin smelt** are one of the most widely distributed species in the Estuary, but they spawn in fresh water in the Delta. Their spawning success is closely tied to Delta outflows, and in the past decade their numbers have declined steadily to the lowest levels ever recorded. **Threadfin shad** is an introduced, freshwater plankivore that is an important prey for striped bass and other fishes in the Delta. Numbers of threadfin shad have shown a declining trend in the past decade or so. In general, planktivorous fishes that live in the Delta and Suisun Bay for significant parts of their life cycle are in decline, while those that have a marine dependence are not.

White croaker. This is the dominant native predatory fish in the Bay, and it can complete its entire life cycle in the Bay, although it is widely distributed in the ocean as well. Overall, croaker numbers have been increasing since 1980 and expanding their range within the Estuary as marine conditions have become more predominant.

Flatfish. The two most abundant species of flounder, English sole and starry flounder, present a contrast in trends. English sole are marine and use the Bay mainly as a nursery area; their numbers show no trend in the past decade but reflect the suitability of oceanic conditions for spawning. Starry flounder are more euryhaline than English sole, and their abundance depends on hydrologic conditions in Suisun and San Pablo bays and perhaps on the presence of toxic substances. Overall, the numbers of starry flounder show a declining trend.

Other fishes. There are numerous other species in the Estuary, but the data on trends are generally limited. In general, marine-dependent species show little or no overall trend in abundance in recent years, while freshwater-dependent species (such as white catfish and Sacramento splittail) show declines. White catfish are one of the most important game fishes in the Delta, while Sacramento splittail are endemic minnows that are declining to the point where endangered status may be justified soon. Bucking these trends is the recently invading chameleon goby, a small oriental species that is rapidly expanding throughout the upper Estuary.

C. Trends in Major Estuarine Regions

Each portion of the Estuary supports characteristic species and is used differently by many of the species that are broadly distributed. The following summaries describe the status and trends of some of the species in each major portion of the Estuary.

South Bay. South Bay was particularly affected by sewage effluent in earlier years but has benefited from provisions of the Clean Water Act. The revived benthic fauna of South Bay (and elsewhere) has allowed development of a clam fishery, which is based almost entirely on introduced species. The combination of extensive shallows with daytime high tides results in high productivity, which permits rapid growth of benthic organisms. Fish assemblages of South Bay are dominated by northern anchovy for most months of the year except winter. Topsmelt, bay gobies, bat rays, walleye surfperch, brown smoothhound, and, especially, adult white croaker, are some of the fishes more commonly found in South Bay than elsewhere. Fishes characteristic of shallow areas are less predictable in abundance than those characteristic of the channels, and generally species occurrences at particular sites and seasons are less predictable than in most other parts of the Estuary. No obvious trends through time or during the recent drought are apparent in the fishes of South Bay.

Secondary habitats of South Bay include large areas of evaporating ponds for salt production and other marshy areas. These ponds go through a succession of stages that support different assemblages of invertebrates and fish, but there are no data on overall trends through time. A number of streams carry fresh water into South Bay; most of these streams have undergone extensive channelization or other alterations that have reduced their ability to support the fish faunas they once did.

Central Bay. Central Bay contains deeper habitats, and a larger percentage of deep habitats, than any other portion of the Estuary. High velocities of water flow in both directions through the Golden Gate each day as the tides move; surface flows of water carry fresh water out of the Bay while denser salt water flows inward along the bottom. Because of these depths and currents, humans have had less impact on the habitats of this embayment than any other. The greatest impacts on aquatic resources would appear to be associated with the dredge spoil site near Alcatraz, but there is little information available to evaluate such effects; whatever effects exist will be reduced as dredge spoil disposal is moved out of the Bay in the future. Fishes of Central Bay are mainly the same species that are abundant

in San Pablo or South bays, most notably northern anchovy. Distinctive fishes of Central Bay are generally more marine species such as Pacific pompano. Anadromous species pass through on a seasonal basis, including chinook salmon and American shad. Pacific herring, which occur in other portions of the estuary, mostly spawn in Central Bay (particularly around Tiburon and Angel Island). Likewise, young-of-year English sole are abundant primarily in Central Bay. The fish assemblages found in Central Bay are very predictable from year to year. Increased dispersal of South Bay species during the recent drought and declining catches of formerly abundant species of San Pablo Bay are apparent in the catches made in Central Bay. However, overall Central Bay fish populations (particularly in bottom trawl catches) show little trend through time, high predictability of species from year to year, and very high species diversity at all seasons.

San Pablo Bay. Like South Bay, San Pablo Bay has extensive shallow areas, but it differs by having large inflows of fresh water which produce a stratified water column. The varying salinities and temperatures of San Pablo Bay appear to restrict the occurrence and abundance of marine fishes characteristic of South and Central bays (such as jacksmelt, shiner perch, and bay goby) to summer months when salinities are highest and least variable. San Pablo Bay has been characterized by regular occurrence and high catches of several euryhaline species: striped bass, starry flounder, longfin smelt, and yellowfin goby. Anadromous species also pass through seasonally. Most of the characteristic species have undergone severe declines during recent years; even fishes that had been among the most abundant (striped bass and longfin smelt) in the past have dropped precipitously. Seasonally present species, other than anadromous forms, have increased in abundance. For example, white croaker were mainly young of year in earlier years, but the stabilization of salinity resulting from reduced year-round inflows of fresh water appears to have led to more regular occurrence of adults. Reduced suitability of upstream nursery grounds and spawning sites and toxic effects of pollutants (at least on starry flounder) may both be responsible for declines in fish abundance. San Pablo Bay appears to be a nursery ground for Dungeness crabs although oceanic conditions, rather than conditions in the Bay, appear to be the dominant control on abundance of adult crabs.

Secondary habitats of San Pablo Bay include streams in the Napa and Petaluma River drainages that support native fishes. Salt ponds around San Pablo Bay support a somewhat different fish fauna than those around South Bay, although they have not been studied in depth.

Suisun Bay. Suisun Bay has been less affected by pollution and dredging than other parts of the Estuary but has been most strongly affected by the introduction of exotic animals and, in the last 20 years, by water development that amplifies the effects of drought. Suisun Bay has been of great importance to several fish species, principally as nursery grounds for young of year. This importance presumably rests on accumulation of food material by interactions of outward-flowing surface currents and landward bottom currents in what is called the entrapment zone. The resulting high densities of food have supported high densities of zooplankton, juvenile fish, and small fish. Most clams in the estuary have not been capable

surviving the highly variable salinities to which the bottom is subjected by movement of the tides. The most recently introduced clam is able to survive these conditions and has rapidly developed extremely high population densities (to 30,000 m⁻²). As a result of the high densities of these clams, densities of chlorophyll and zooplankton have been extremely low. Populations of most fish species that use the nursery areas of Suisun Bay declined prior to the spread of the newest clam. Extended drought conditions, coupled with record rates of diversion, resulted in restriction of the entrapment zone to deeper channels near the upstream end of the bay. In addition, net reverse flow in the lower San Joaquin River, which had previously been a feature of summertime conditions, became a regular feature for most of the year. These net reverse flow conditions now occur during the spawning season of several species found in Suisun Bay which move upstream to spawn; hence movement of the larvae by currents has been away from the entrapment zone in recent years. The material, zooplankton, and fish in the entrapment zone are also moved by the tides up into the river channels where they may suffer further entrainment.

Species characteristic of Suisun Bay, and which have sharply declined over the last decade, include Delta smelt, longfin smelt, striped bass, and yellowfin goby. Northern anchovy are much less common in the catch than at sites below Carquinez Straits. White sturgeon are a predictable catch in Honker Bay. The opossum shrimp (*Neomysis mercedis*) is abundant in the entrapment zone and is very important in the diet of most fish species in the bay.

An important secondary habitat of Suisun Bay is Suisun Marsh. Suisun Marsh has recently supported high densities of native fishes, including Sacramento splittail and tule perch, that are not abundant elsewhere in the estuary.

Delta. The Sacramento-San Joaquin Delta has a long history of intensive modification. More than 95% of the original tidal wetlands have been eliminated. Dredging of channels has put large portions of the water column beyond the reach of sunlight and has caused the water to flow much more rapidly through its channels. Over 1500 local agricultural diversions are unscreened so that they represent a serious hazard to larval fish. Increasing diversion of fresh water by the State and Federal operations from the south Delta alters the direction of flow in several main channels. Agricultural and urban runoff are the principal sources of pollution.

Fishes of the Delta are predominantly the introduced striped bass, catfishes, sunfish, crappie, threadfin shad, and carp. Native fishes are generally found in shallower sloughs near the Sacramento River but these habitats are not sampled in any regular sampling program. Bottom animals include several introduced species of crayfish and clams, that are known to occur in high densities (crayfish are collected commercially), but little is known of their population biology. Populations of many invertebrates and most fishes in the Delta have declined in the past 25-30 years. Invertebrates that have shown declines are mostly planktonic species, including rotifers, cladocerans, and native copepods. Among the fishes, populations of delta smelt, longfin smelt, and splittail have declined to extremely low levels

and may qualify them for listing as threatened or endangered species. Striped bass and chinook salmon have declined to the point where their fisheries are now at only a fraction of what they were even 20-30 years ago. Even supposedly robust resident introduced fishes, such as threadfin shad and white catfish, appear to have declined in abundance. Entrainment or displacement due to effects of the Central Valley Project and State Water Project diversions appear to be the major cause for the declines of most species, although other factors contribute to mortality. For striped bass the effects of increased concentrations of toxics in the water at the time and place of spawning also coincides with the sharpest period of their decline.

III. Productivity and Aquatic Resources

The first step in assessing food availability to higher organisms in the Bay is a systematic accounting of organic carbon sources. These sources include growth of food material within the Estuary (autochthonous sources), food material carried in on water currents from nearby ecosystems (allochthonous sources), and net contributions by horizontal transport among different habitats within the Estuary. In order to assess these sources the Bay was divided into South, Central, San Pablo, and Suisun bays. Hypsographs and related morphometric data were assembled for each of the four subembayments. Estimates were made of each organic carbon source for each subembayment using a variety of techniques. Phytoplankton productivity was estimated from a morphometric model and measurements made in 1980. Benthic microalgal productivity, seagrass productivity, and tidal marsh export were estimated from habitat area in conjunction with the range of values (on the basis of unit area) published for other estuaries. Delta discharge, point sources, nonpoint source runoff, atmospheric deposition, spills, and dredging sources were all estimated from data collected for San Francisco Bay. Macroalgal productivity, photosynthetic bacterial productivity, ground water contributions, and biotic transport could not be estimated quantitatively, but were assessed on the basis of qualitative considerations. Transport due to circulation and mixing could not be estimated.

The available data permitted a comparison of the different carbon sources only for 1980. Phytoplankton productivity, benthic microalgal productivity, and Delta discharge of organic matter probably were major sources (>25%), although their importance differed among subembayments. Tidal marsh export, point sources, and dredging transport probably were significant secondary sources (>10%). Seagrasses, macroalgae, photosynthetic bacteria, runoff, atmospheric deposition, spills, groundwater, and biotic transport appear to have been minor sources (<10% total), regardless of subembayment.

For San Francisco Bay as a whole, phytoplankton productivity was the dominant source of organic carbon (50%) while benthic microalgal productivity was the only significant secondary source (20%). All other sources contributed less than 10% of the total.

comparisons for the whole Bay, as well as for each subembayment, assume that only about one-tenth of Delta discharge was actually available to the food web.

For South Bay, phytoplankton productivity was the dominant source of organic carbon (60%) in 1980, but benthic primary productivity was probably a major source (30%) as well. Since 1980, annual phytoplankton productivity in the photic zone of the channel has fluctuated within a factor of two, but no long-term trend were observed. Productivity tends to increase with annual Delta discharge, apparently because higher Delta outflow promotes stratification of South Bay waters. Stratification, in turn, leads to higher algal growth rates and lower losses to suspension-feeding benthic macroinvertebrates. Productivity thus may remain low as long as Delta outflow is depressed. The lack of long-term production data for shoal phytoplankton (accounting for 60% of total phytoplankton productivity) and benthic microalgae prevents more certain conclusions.

For Central Bay, phytoplankton productivity (40%) and benthic microalgal productivity (30%) appear to be the major sources of organic carbon. Point-source loading (10%) and transport of dredging spoils from adjacent subembayments (10%) could be significant secondary sources. Insufficient data exist to characterize interannual variability of phytoplankton or benthic microalgae since 1980. The available evidence suggests that mechanisms for phytoplankton variability in Central Bay are different from those in South Bay and San Pablo Bay, including possibly a major influence from the ocean. Point-source loading continued to decline after 1980. Dredging effects are hard to discern because they exhibit much interannual variability, but no trend. The boundary used to delimit South Bay from Central Bay needs to be reconsidered for analytical purposes.

San Pablo Bay was dominated by phytoplankton productivity (60%) in 1980. Benthic microalgal productivity (20%) and marsh export (20%) may have been significant secondary sources of organic carbon. No long-term data exist for shoal phytoplankton, which accounted for almost 80% of the estimated phytoplankton productivity. However, the mechanisms controlling interannual variability in San Pablo Bay are thought to be similar to those in Suisun Bay.

For Suisun Bay the dominant organic carbon source probably was riverine loading from the Delta (60%) in 1980, even when only one-tenth is considered available as food. Marsh export (20%) and phytoplankton productivity (10%) may have had a secondary role. Much of the organic matter contributed in Delta discharge seems to have been phytoplankton and its breakdown products. The drought period that began in 1987 has depressed Delta outflows and, presumably, riverine loading of organic matter as well. Phytoplankton productivity has been low since 1983. The low phytoplankton productivity has been attributed to two mechanisms. First, the entrapment zone, which retards advective losses of phytoplankton from its vicinity, is absent during periods of extremely high or low Delta outflow. Second, suspension-feeding estuarine invertebrates become established during periods of prolonged drought and are responsible for increased grazing losses. Tidal marsh export could actually be a major organic carbon source at present.

The invasion of the corbulid clam *Potamocorbula amurensis* in 1987 may lead to the persistence of high grazing losses even after the drought ends, due to the clam's tolerance of low salinity water. If so, local productivity could remain low, and riverine loading (and tidal marsh export) would be even more important as an organic carbon source.

Overall, evidence from hydraulic residence times, benthic invertebrate consumption rates, and oxygen consumption suggests that most organic carbon sources in the South Bay, Central Bay, and San Pablo Bay enter the food web. On the other hand, organic carbon sources for Suisun Bay--particularly riverine loading--may actually be consumed downstream in San Pablo Bay or upper Central Bay. Based on empirical generalizations from a synthesis of work at other estuaries, as well as from the apparent importance of food supply for zooplankton in Suisun Bay, a decline of fish production in the upper estuary can be expected to have accompanied the decline of organic carbon sources since the early 1980s. During drought conditions, relatively more of the organic carbon supply is probably shunted through benthic, rather than planktonic, pathways, favoring a relative increase in demersal organisms. Because water diversions from the Delta have been proportionally higher during the drought years, export of organic matter may also be contributing to the decline of the fishes and other aquatic resources.

IV. Information needs.

If the Estuary is ever going to be restored to a productive, predictable system that supports the major fisheries it has in the past, we need to develop an understanding of how the Estuary functions as an ecosystem. Development of a general descriptive model of the estuarine ecosystem is necessary. Attention to date has focussed on a few species or on particular areas, with little coordination among studies. Species have received attention largely in a crisis management situation: collapse of fisheries in the Bay was handled by eliminating most commercial fisheries; declines of salmon and striped bass were addressed by rearing fish in hatcheries; entrainment of fish in the pumps of big water projects was dealt with by trapping and trucking; focussed studies of Delta smelt began only when it was proposed for listing as an endangered species. The declines of numerous species in the Estuary, at all levels of the food web, should be convincing evidence that there is a general environmental problem rather than a series of species-specific problems. Solving the problem from a unified and scientific approach is likely to be more effective and efficient than a piecemeal approach. Some of the major components of such a unified study would include:

1. Determine the patterns of use for all major species in the Estuary, regardless of economic value.
2. Determine the productivity of various parts of the Estuary and identify the sources of energy for aquatic food webs.
3. Determine the trophic connections among the aquatic resources. In other words, describe the food web.
4. Identify the sources of mortality and mortality rates for representative species in each habitat.

5. Develop an understanding of how introduced species invade the Estuary to establish procedures for prevention and control.
6. Determine how major changes to the Estuary, such as flooding Delta islands or changes in diversion rates, would affect the aquatic resources.

Background Overview and Glossary

An estuary is a partly enclosed body of water where sea water and fresh water meet, San Francisco Bay is divided into a number of smaller **embayments** such as Suisun Bay. Many estuaries are important nursery grounds for fish. **Salinity** of the water in an estuary indicates how diluted the sea water is. Sea water normally has a salinity of 3.5 per cent, but it is usually given in parts per thousand (**ppt**); $3.5\% = 35\text{ppt}$. Fresh water normally has less than .5 ppt so salinity generally goes from 35 ppt at the mouth of the estuary to 0 in the inflowing rivers. Fresh water coming from saline soils may carry relatively high concentrations of salts (and other contaminants) but these salts are seldom exactly like those found in sea water and their concentrations are usually spoken of as **total dissolved solids (TDS)** rather than salinity. The amount of salt in water can be measured by how easily it allows an electric current to pass, this measure is called the **electrical conductivity**. Many fish are found only in water with particular levels of salinity, TDS, or electrical conductivity, fish which can tolerate a wide variety of salinities are said to be **euryhaline**.

River and ocean currents modify how much material is carried into the estuary. High river flows in wet years carry more material downstream, although the concentration in the river water may not increase. River flows may be spoken of in terms of the quantity of water they transport or in terms of the rate at which they carry water. Quantities of water are often referred to in **acre-feet**, which is equal to an amount of water one acre in area and one foot deep. Rates of water flow are usually given in cubic feet per second (**cfs**). A rate of flow at 1 cfs will provide about 2 acre-feet in the course of a day. In the Sacramento-San Joaquin Estuary large quantities of water are **diverted** so that there is a large difference between the amount of water flowing down the rivers (**delta inflow**) and that which flows into the bay (**Delta outflow**). **Upwelling** currents bring material up from the ocean floor and make it available for transport into the estuary by tidal and other currents. In addition to daily tidal cycles, tidal currents vary on a biweekly basis between strong **spring tides** and weaker **neap tides**, as well as on a seasonal basis. There will usually be areas within the estuary where fresh water flows downstream on top of a bottom layer of sea water, rather than mixing with it. This phenomenon is called **stratification** and may have significant ecological impacts, for instance clams or other **molluscs** on the bottom will not be able to filter food from the upper level of fresh water and plants may be able to grow to greater densities than they can in the absence of stratification.. At times of higher outflow there will usually be more stratification.

Food can be grown in the estuary by the plants that live there or it may be carried in on currents from upstream or from the ocean. Within the estuary most food production is due to small plants that float in the water; these often single-celled algal plants are called **phytoplankton**. Growth of phytoplankton in the estuary is often controlled by how much sunlight each plant is exposed to; below a certain depth (**the photic depth**) plants cannot get enough light to sustain growth. Wind-generated or other currents may resuspend phytoplankton into the **photic zone**. Growth of phytoplankton is also controlled by how quickly they are transported through an area; short **residence times** usually mean low

phytoplankton density. The quantity of phytoplankton is usually quickly estimated by measuring the quantity of **chlorophyll a** in the water since all plants contain this green pigment. The quantity of phytoplankton (its **biomass**) may have little to do with how fast it is growing (its **productivity**) if it is eaten quickly by animals. Phytoplankton may be carried in on currents along with other small pieces of organic material; these particles of potential food are called **particulate organic carbon (POC)**. In contrast, organic material that is dissolved in the water is called **dissolved organic material (DOC)**. Comparison with a glass of lemonade can clarify the difference--the sugar is DOC and the fragments of lemon are POC. Many of the small animals that float in water feed on POC but only bacteria and a few other organisms can absorb DOC.

The organisms that float in the water and consume, mostly, POC are called **zooplankton**. Some may be single-celled animals or very small multi-cellular animals (**microzooplankton**). Phytoplankton and microzooplankton are eaten by larger zooplankton which are in turn eaten by fish. Most of the larger zooplankton are the various relatives of shrimps called **crustaceans**, usually **copepods** in more saline waters and **cladocerans** in fresher water. Organisms that live in or on the bottom are called the **benthos**. Many are **molluscs** which filter food from the water. Moving along the bottom and eating material that has settled to the bottom are **epibenthic** crustaceans like crayfish, shrimp, or crabs. Benthic and epibenthic animals are particularly likely to develop high concentrations of pollutants in their bodies.

Most estuaries show a strong seasonality in the abundance of phytoplankton and zooplankton. Most fish species which use estuaries for nursery grounds spawn just prior to the onset of seasonal peaks in plankton biomass. Fish that feed on plankton are called **planktivores**; fish that eat fish are called **piscivores**. Many of the widely known fish of the estuary migrate upstream to spawn. This **anadromous** habit serves to bring the sexes together and allows the young fish to grow in shallow habitats which are scarce in the Bay and ocean. Under present conditions in the Delta a large fraction of the inflowing water is diverted for local use or export and anadromous species suffer **entrainment**, the capture or displacement of migrating individuals by diversion.

1 Physical Background of Sacramento-San Joaquin Estuary

1.1 Geologic setting

The Sacramento-San Joaquin Estuary is unlike any other river mouth in several significant ways. The Estuary is the product of very recent geological activity. Uplift of the Coast Range blocked or diverted the flow of what had been a long series of independent coastal streams into a complex drainage with two main rivers flowing through the newly formed Central Valley (Atwater 1980). The resulting summation of the American, Cosumnes, Feather, Kern, Kings, McCloud, Merced, Mokelumne, Pit, Sacramento, San Joaquin, Tuolumne, Yuba, and other rivers produces the 25th largest outflow in North America from a drainage area that receives almost no rainfall for half of the year. The only escape for this outflow is a narrow notch in the Coast Range. Thus, the river channels must coalesce and narrow as they approach the sea, unlike most other deltas where channels split and spread over a broad flood plain.

Narrowing of the channels closest to San Francisco Bay and a highly seasonal pattern of outflow give the river tremendous hydraulic power so that its geological effects are disproportionate to its age. The river carved its way through low points in two series of hills and produced one of the most perfect natural harbors in the world. The three right-angle bends, that the outflowing water must negotiate on its way from the Delta through Carquinez Straits to the Golden Gate, produced three large eddy pools, Suisun Bay, San Pablo Bay, and South Bay. Local outflow in these areas (e.g. principally Denivert Creek into Suisun Bay, Petaluma and Napa rivers into San Pablo Bay, and Alameda and Coyote creeks into South Bay) played a much smaller role in shaping the topography of these areas because they contribute less than 10% of the water entering the Bay. In this document "Bay" refers to Suisun, San Pablo and San Francisco bays; "lower Bay" refers to the Bay below Carquinez Straits; "Delta" refers to the Sacramento-San Joaquin Delta within the area encompassed by Antioch, Vernalis, and Sacramento; and "Estuary" is used as the collective term.

The soil of most estuaries consists of deep layers of fine sediments carried from upstream. During the dry season sediments settled out in the Delta, although wind action is likely to have resuspended and redistributed them. Thus, the Delta acted as a large settling pool, and islands developed as sediment-laden waters spread over higher ground, slowed down as they flowed among cattail and tules, and deposited their minerals along the edge. In this fashion the islands grew to resemble atolls. Growth of vegetation in the centers of these islands led to extensive development of peaty soils. In the wet season many sediments were transported all the way through the Delta and Bay to form large shoals in the Gulf of the Farallones. Within San Francisco Bay, mudflats are most abundant in the eddy-like portions of Suisun, San Pablo, and South bays. Central Bay contains much deeper areas than the other embayments (>99 m) and has few shallow areas (Fig A.2) because high outflows periodically provide high flushing rates. Depths within the Bay range from large shallow

areas where sediments have accumulated to quite deep areas that are subject to high current velocities.

Glacial action brought layers of glacial sediments into the Delta so that soils interfinger deltaic sediments with layers of sand and gravel (Shelemon and Begg 1975). Burial and decomposition of large quantities of marsh vegetation yielded several areas where natural gas is abundant enough to be mined (Safanov 1962).

Tectonic movements have raised and lowered the passes through which river water must flow on its way to the sea. At times the notch in the Coastal Range has been as much as 40 m above sea level. Thus, for much of the recent history of the Estuary, inland waters could only have flowed out for a short part of the year. The isolation of the Bay from the Delta has produced a sharply segmented Estuary, with a Bay ecosystem dominated by marine taxa and a Delta dominated by freshwater forms. Most of the intensively studied estuaries of North America are on the Atlantic coast, and they possess a long, shallow, braided channel where marine and freshwater influences interact. The Sacramento-San Joaquin Estuary is similar to other estuaries of the Pacific Coast where most major rivers run into the ocean with limited areas of tidal marshes and other features typical of older estuarine systems.

1.2 Freshwater outflow, marine currents, and hydrology

1.2.1 Estuarine conditions

Picturing the Estuary as a simple conflict of riverine vs. marine influences hides the complex interactions of hydrology, biology, and human influences. Although net water flow is from east to west, flow conditions change tidally, seasonally, and annually in response to oceanic conditions and upstream rainfall patterns. Patterns of flow also differ among the four major embayments. Thus, the lack of a natural deep channel through South Bay gives it the characteristics of a lagoon estuary, while the entry of most fresh water into Suisun and San Pablo bays give them the characteristics of a partially mixed estuary. San Pablo and Suisun bays are components of a North Bay, that is quite different from South Bay or the more oceanic Central Bay. Human activities alter flow velocities, volumes, and even direction in the sloughs and river channels of the Delta. Water management strategies in the Central Valley also affect hydrology and biology in San Francisco Bay.

The height of the Sierra Nevada usually leads to much of the precipitation falling as snow. This snowpack greatly moderates outflow from rivers of the Central Valley in comparison to coastal streams, such as the Russian or Eel rivers, where rainstorms are followed immediately by high outflow. Air temperature during storms affects the percentage of precipitation falling as rain or snow; warmer precipitation leads to greater immediate runoff and lower runoff later in the year. The Sierra snowpack reduces the suddenness of peak outflows and stretches the period of high outflow over several months. Nevertheless, prior to human intervention, outflow from the Delta usually fell to very low levels for several months preceding the onset of the next wet season. The low-lying Delta thus

supported extensive wetlands, including ponds, sloughs, marshes, and a riparian strip along the rivers that was as much as 40 miles wide. Very low summer outflow permitted annual incursions of brackish water into the Delta.

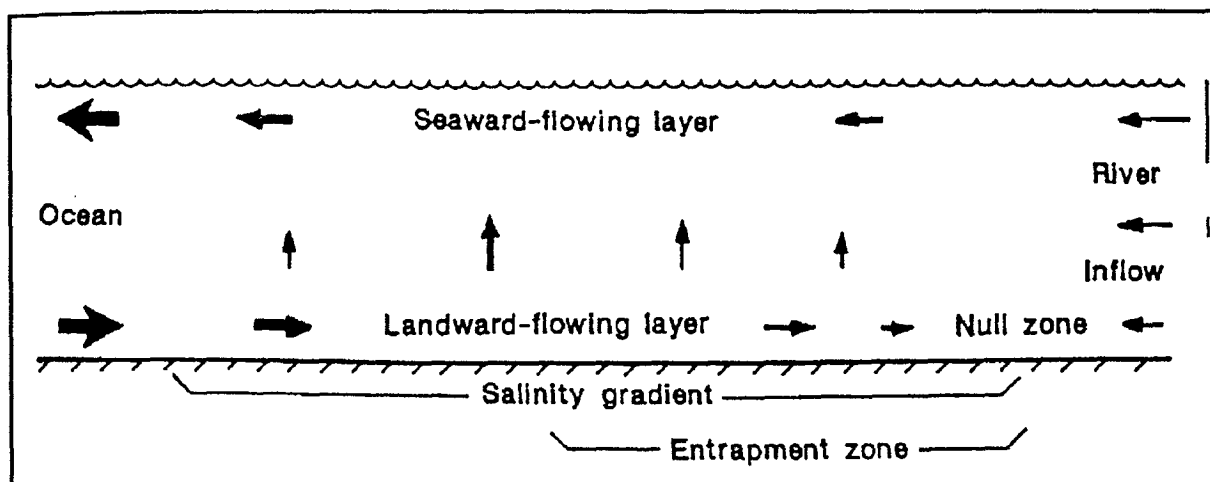


Figure 1 Greatly simplified diagram showing hydraulic patterns producing the entrapment zone. Width of arrows indicates intensity of flow. Modified from Jones and Stokes 1990.

Outflowing fresh water produces several ecologically important conditions in San Francisco Bay. Sea water flows in to displace fresh water from the bottom. Thus, a bottom current of marine water often flows into the Bay while a lens of fresh water floats seaward on the surface. Either current, or both, may form eddies and deposit sediment in areas where topography causes the current to slow. Between the two currents is a plane of water exhibiting little net movement upstream or downstream. Mixing between the two currents increases as the bottom current proceeds upstream, and at some point stratification breaks down (Figure 1). Landward-flowing bottom currents receive a variety of sediments and planktonic organisms as the seaward-flowing surface currents slow down. The breakdown of stratification reunites these sediments and plankton with the surface currents. Recycling of these sediments, with their advected nutrients, produces an area where some species of planktonic algae accumulate and may benefit due to the high concentration of nutrients. Incorporation by algae, ingestion by animals, or simple flocculation can all contribute to entrapment of riverine materials in this area. Prolonged residence times, due to the mixing of currents and the reinoculation of phytoplankton from downstream permits the build-up of high algal concentrations characteristic of this area. Similar mechanisms, augmented by behavioral traits, lead to concentration of zooplankton and fish in this area. In this report this region of high concentrations of suspended particles resulting from an equality between bottom and surface currents as the "entrapment zone" although it is often also called the "null zone."

Generally, strengths of bottom currents mirror the strength of outflow. Under high outflow conditions bottom currents are stronger; low outflows of fresh water provide little stratification and bottom currents tend to be weak. Seasonal variation in tidal flows, and the consequent different volumes and velocities of the tidal prism, can greatly modify the effects of density-driven currents. With extremely high outflows, stratification occurs downstream of Carquinez Straits and the depth and volume of the downstream embayments prevents formation of a mixing zone. Within a broad middle range of outflows, bottom currents penetrate upstream into Suisun Bay or the lower river channels. Presence of the entrainment zone in the extensive shallow regions of Suisun Bay increases the residence time of phytoplankton. The resulting greater concentration of phytoplankton has often been cited as essential for planktonic fish larvae to survive (see Appendix A).

Flow patterns have become less variable in the Delta since the construction of dams on the tributary rivers. Seasonal water temperatures and salinities in the Delta have also become less variable as a consequence of the decreased seasonality of flow.

1.2.2 Tidal flows

Tidal flows affect the primary productivity of the estuary and the productivity of its aquatic resources in many ways. On an average tidal cycle the volume of sea water entering the Bay, the tidal prism, is roughly equal to 24% of the volume of the Bay. The twice daily tidal cycle (mixed semi-diurnal) directly transports oceanic materials, nutrients, and biota through the Golden Gate. In addition, the waters of the various subembayments are also moved through different habitats and among basins. The entrainment, consumption, or other use of these transported materials can produce a net flow of materials despite the cyclical movements of water. Thus, in the spring, water flowing out of the Bay on a receding tide may pick up nutrients from upwelling currents and bring them into the Bay on its return. Contrarily, tidally transported water from the Bay in the winter may be replaced with nutrient-poor water. At the other end of the estuary, tidal currents can regularly move planktonic animals within range of entrainment by various diversions in the Delta. The magnitude, or even the net direction, of any such transports is largely unknown.

Transport among embayments and the important effects of tidal transport of water through marshes and other habitats will be discussed below in terms of the movement of fixed carbon. The main pattern of importance to animals is that, due to the deep channel connecting Central, San Pablo, and Suisun bays and the Delta, a greater volume of water is moved by tidal action through the Northern Bay than through South Bay. Corollary to this is that the South Bay has the largest amount of tidal mudflats (Nichols and Pamatmat 1988). Primary productivity of the South Bay tidal mudflats is increased because more of the spring low tides occur during daylight hours so that the benthic algae receive the maximum insolation during their principal period of growth (Nichols and Pamatmat 1988). In other parts of the estuary tidal actions interact with other environmental variables to produce synergistic effects that are difficult to anticipate from consideration of one factor at a time.

Tides directly affect aquatic animals in two main ways. The twice daily influx of ocean water subjects stationary animals to a strongly varying salinity regime in most of the Bay. This effect is strongest in Suisun Bay where fresh water presents an entirely different osmotic problem than brackish water. The changing salinity of Suisun Bay is thought to have been a major factor in preventing the development of a large benthic fauna there (Nichols and Pamatmat 1988). This idea developed from observing the invasion by large numbers of the clam *Mya arenaria* when the water remained salty during the drought in 1976-77 and their rapid disappearance upon the return of normal river flow (Nichols 1985). The idea has received additional support by the recent invasion and rapid population growth of the euryhaline clam *Potamocorbula amurensis*.

The effects of tides on aquatic resources are also strongly influenced by the behavior of tidally transported animals. For example, by sinking to the bottom for part of the tidal cycle and swimming into the water column during the other part, even small animals can migrate long distances. Since tidal flows approach 3 ms^{-1} such migrations can proceed quickly. The presence of a tidal cycle every twelve hours also permits benthic animals, particularly shrimp, to combine their use of tides for migration with a need to minimize predation by being out of the substrate only during the night (Siegfried et al. 1978).

1.2.3 Winds

Winds play an important role in resuspending bottom accumulations of nutrients, organic material, and organisms, particularly the larger species of phytoplankton. The effectiveness of winds in disrupting stratification and in reinjecting bottom material into the water column is a function of the topography of the embayments and the strength and direction of the winds. In the deepwater channels and in most of Central Bay, the water is too deep to permit much mixing, whereas water over the shoals of South Bay, Suisun Bay, and San Pablo Bay can often be thoroughly mixed. Winds in the Bay area are seasonal with strong westerly or north-westerly winds in the summer (Conomos et al. 1985).

Large shallow areas and strong winds provide a thorough oxygenation of most Bay waters (Hartman and Hammond 1985). Unlike most other estuaries, the oxygen concentration profiles in the Bay show saturation with oxygen all the way to the soil-water interface. Until the 1960s, this thorough mixing was often overwhelmed by the high biochemical oxygen demand (BOD) of organic matter discharged into the Bay in crudely treated waste water. The lower rates of water exchange of South Bay with the ocean or with other embayments led to pronounced problems of low oxygen concentrations available to benthic organisms (Skinner 1962).

1.2.4 Oceanic processes

The northwest to southeast slant of the California coastline is interrupted by the outthrust of Point Conception. Generally, the coast below Point Conception is under the influence of the northward flowing Davidson Current, which brings subtropical waters northward. At

Point Conception these waters meet the southward flowing California Current which carries subarctic waters. These very different currents produce profound differences in the biological communities they support with, for instance, tropical fish families populating kelp forests off southern California whereas similar kelp forests in northern California are occupied by temperate zone families (Foster and Schiel 1985). Near San Francisco Bay, the oceanic conditions respond markedly to the shifting strengths of the Davidson and California Currents and the coastal zooplankton populations fluctuate in response (Hatfield 1983a).

Oceanic conditions vary in most years through three seasonal stages: the upwelling period, the oceanic period, and the Davidson Current period (Skogsberg 1936; Bolin and Abbott 1963; Wild and Tasto 1983). *El Niño* events are usually associated with the failure of this seasonal progression. The most significant ecological impact is associated with the strength of the upwelling period from March through August. At this time, strong northwesterly winds and southerly surface currents produce offshore Ekman transport of nutrient-poor surface water and its replacement along the coast by nutrient-rich bottom water. The strength of the upwelling is closely tied to the abundance and species composition of the near-shore zooplankton community (Peterson 1973; Peterson and Miller 1975; Peterson et al. 1979; Hatfield 1983a). The oceanic period marks a shift in climatic conditions, there is a lull in winds and water flow in September and October. In November, southerly winds and the north-flowing Davidson Current produce a downdraft of surface waters along the coast. The vertical movement of water causes surface temperatures to decline during upwelling and causes deeper water temperatures to rise during the late fall and winter. Upwelling is strongest near San Francisco Bay during June and July (Bakun 1975).

Year-to-year changes in oceanic conditions are a result of large-scale meteorological activity. The most striking recent fluctuation occurred during *El Niño* conditions of 1983. Warmer tropical waters at the surface produced density differences between surface and bottom waters which were too strong to be broken down by Ekman transport. Consequently there was little upwelling, and productivity at all trophic levels was reduced. Upwelling may also be important in reinforcing the circulation of bottom currents into the bay, whereas Ekman transport of surface waters promotes onshore movement of surface water and reduce estuarine circulation (Peterson et al. 1989). Pacific herring was one species whose decline under *El Niño* conditions of 1976-1977 and 1983 was well documented. These conditions in 1983 were accompanied by massive storm systems and record-setting precipitation of rain and snow. The resulting high outflows led to water residence times that were very short and productivity that was very low. In addition, the entrapment zone was far downstream of its normal position. Thus, low oceanic productivity lowered the marine contribution of productivity to the estuary at the same time that riverine production was small and hydrodynamic processes failed to produce the usual accumulation of fixed carbon.

Year-to-year variations in oceanic conditions, particularly upwelling, are thought to control recruitment success in a number of marine species. However, there does not appear to be any periodicity to the strength of upwelling while there is obvious periodicity in populations of Dungeness crab, coho salmon, or chinook salmon (Botsford et al. 1982).

Multi-year changes in oceanic conditions have also been recorded with corresponding changes in the abundance of aquatic resources. In the years following 1957 mean ocean water temperature and mean sea level rose in response to the greater influence of subtropical ocean waters and stronger southwesterly winds (Huang 1972; Namias and Huang 1972). Not surprisingly, these conditions particularly strengthened the conditions associated with the Davidson Current (Sette and Isaacs 1960). Dungeness crab is one species that apparently responded to this general change in conditions (Wild et al. 1983).

Major Factors Affecting Aquatic Resources

2.1 Introduction

Under natural conditions, the Estuary was a highly variable system. The seasonal patterns of freshwater inflow were predictable in general timing. High inflows followed snow melt from the Sierras in the spring and dropped to a low point in autumn. However, the amount of freshwater inflow and its exact timing within the spring season was enormously variable. Likewise, the occurrence of high tides in spring and fall is a highly predictable occurrence but the extent to which the tides push salt water into the estuary depends on both the amount of outflow and the strength of the winds blowing at the time. While this natural variability has been damped somewhat through human control of freshwater inflow, other human impacts on the estuary have made the estuary an increasingly difficult place for large populations of most organisms to persist. The most severe changes were the result of the combined effects of agricultural development, hydraulic mining, and the introduction of exotic species, although other factors, such as urban development and exploitation of some species played a role as well. In the following sections we discuss in general terms the effects of:

- (1) natural variability in precipitation
- (2) water development
- (3) pollution
- (4) waterway modification (including diking, dredging, mining, and siltation)
- (5) introduction of aquatic organisms
- (6) exploitation.

2.2 Natural variation in flow to the Bay and Delta

The most commonly cited control on abundance, distribution, and reproductive success for many species of fish in the Sacramento-San Joaquin estuary is the quantity of river flow through the Estuary (Goldman 1970; Turner and Chadwick 1972; Peterson et al. 1975; Chadwick, et al. 1977; Conomos 1979; Kjelson et al. 1981; Herrgesell et al. 1983; Stevens and Miller 1983). Flow affects aquatic resources in myriad ways. Some species spawn most successfully on flooded vegetation, which is more available in years of high outflow (Daniels and Moyle 1983). Recruitment of some anadromous species is much higher when high outflows provide access to additional spawning habitat. Many anadromous species and

marine species that spawn in the Bay require a sufficient plume of freshwater to allow them to find their way into the Golden Gate. River water carries nutrients into the estuary and low nutrient loading may, at times, limit local (autochthonous) production (Ball 1989). River water increases its load of phytoplankton as it approaches and passes through the Delta (Greenberg 1964). The importance of such imported (allochthonous) production for Bay ecosystems is unknown, but possibly great (Appendix A). Outflow controls the bottom marine currents carrying many young ocean-spawned fish and invertebrates into the Bay. The interaction of outflow with marine currents controls whether the entrainment zone is located in the shallow topography of Suisun Bay or in the deeper channel areas upstream or downstream.

The volume of water flowing into the Delta is extremely variable across years (Figure 2). Years close to the average are less common than those much wetter or drier. The last 15 years have encompassed the wettest year on record (1983) and the wettest month on record (February 1986). Two of the longest and driest droughts on record also fell in this period (1976-1977 and 1985-present). During the drought year of 1990 the Central Valley also experienced the wettest May on record. There is no appreciable autocorrelation of outflow in one year with outflow in the preceding year ($r=.10$). However, within a year, outflow from month to month is strongly autocorrelated ($r=.68$), so a year of high outflow typically has high outflows across several months; wet months during dry years, like February 1986, May 1990, and March 1991 are less common.

Studies of the fishes of the Sacramento-San Joaquin estuary have focussed on identifying those species characteristic of different outflow conditions. Stevens and Miller (1983) identified high outflows as supporting higher populations of American shad, longfin smelt, and chinook salmon. Armor and Herrgesell (1983, 1987) identified several abundant species as characteristic of wet years or dry years. Pearson (1989), for several species in the South Bay, differed with the findings of Armor and Herrgesell.

The possible mechanisms by which flow variability, either in the rivers or in the estuary, could control fish recruitment were summarized in Stevens and Miller (1983):

1. Low flows during incubation following high flows during spawning often results in dewatering of salmonid redds, causing mortality of eggs, embryos, and alevins of salmon. Many other fishes spawn around submerged objects, and their adhesive eggs would then be subject to the same sort of mortality during years with sharp differences in outflow across a short time span.
2. Low flows expose a higher proportion of fish populations to possible entrainment by water diversions. A higher proportion of water is taken in years of low inflow, and greater numbers of fish are entrained.
3. Smaller river volumes increase the density of young fish in the river channels, thus permitting more efficient foraging by predators.
4. Moderately high flows increase the diversity of habitats available, especially increasing the availability of shallow habitats where young fish enjoy greatly reduced predation pressures.

5. Moderately high spring/summer flows increase zooplankton abundance in the Bay, resulting in more food available for larval striped bass and smelt.

The multiple effects of outflow on aquatic resources are mirrored in the adaptations of many native species. The dominant fishes in the Sacramento-San Joaquin Delta are minnows (Cyprinidae). California's minnows are exceptionally large and can postpone breeding in dry years. The energy saved by not breeding is put into growth so that older fish can be quite large (> 1 m) and, because fecundity is size dependent, very fecund in years of high outflow. Large size also probably permitted widespread movements of individuals so that streams dewatered in dry years could be rapidly recolonized by downstream populations. The two small native cyprinid fishes (speckled dace, *Rhinichthys osculus*, and California roach, *Lyvinia symmetricus*) are not found in the estuary. Splittail are one of the most euryhaline minnows, reflecting the formerly frequent intrusion of salt water into the Delta.

Recent changes in outflow that have had obvious impacts on aquatic resources are the severe drought of 1976-1977, the dry year of 1981, the record setting wet year of 1983 (accompanied by dramatic changes in oceanic conditions), and the drought of 1985 to the present, which was interrupted by the wettest month on record in February of 1986. Although global warming is popularly supposed to be revealed in the increasing frequency of drought conditions, tree ring studies have shown that California has had numerous periods of extended drought. Recent conditions may simply reflect the generally episodic nature of California's climate; a mean outflow can be calculated, but few years are close to the mean, and outflow usually changes greatly from year to year.

2.3 Water development

Rerouting of water within the Central Valley was one of the first impacts of early agriculture and mining. Lakes that used to form in low areas of the San Joaquin Valley were drained and their beds were diked and farmed. River flows were captured, stored, and released according to the needs of humans, natural hydrologic patterns were disrupted. Within the Delta the direction of water flow in channels changes in response to diversion practices. Direct impacts of water diversion on aquatic resources include: entrainment of all life stages, transport of species into new areas, changes in the distribution of temperature and conductivity isolines, alteration or confusion of migration patterns of spawning adults or migrating young, and entrainment of organic carbon sources for the food web.

Although construction of each diversion facility is a separate historical event, the effects of diversion produce one of the few linear trends apparent in the hydrologic features of California. The correlations within the estimates of river flow, export rates, precipitation, and other hydrologic data contained in the DAYFLOW program of the State Department of Water Resources can be grouped into two main principal components. Flows in each of the rivers, precipitation, and total delta outflow covary as a unit and account for more than 90% of the measured variability. The association of export rates with increasing year constitute the second principal component and account for most of the remaining variance. The tight

correlation of export volume with year makes it difficult to separate the effects of diversion from other linear changes, such as increasing urbanization, that may account for a portion of the observed changes in fish abundance through time. To address this problem we suggest effects of diversion that may be responsible and then examine different species or different areas to attempt to corroborate the proposed mechanism.

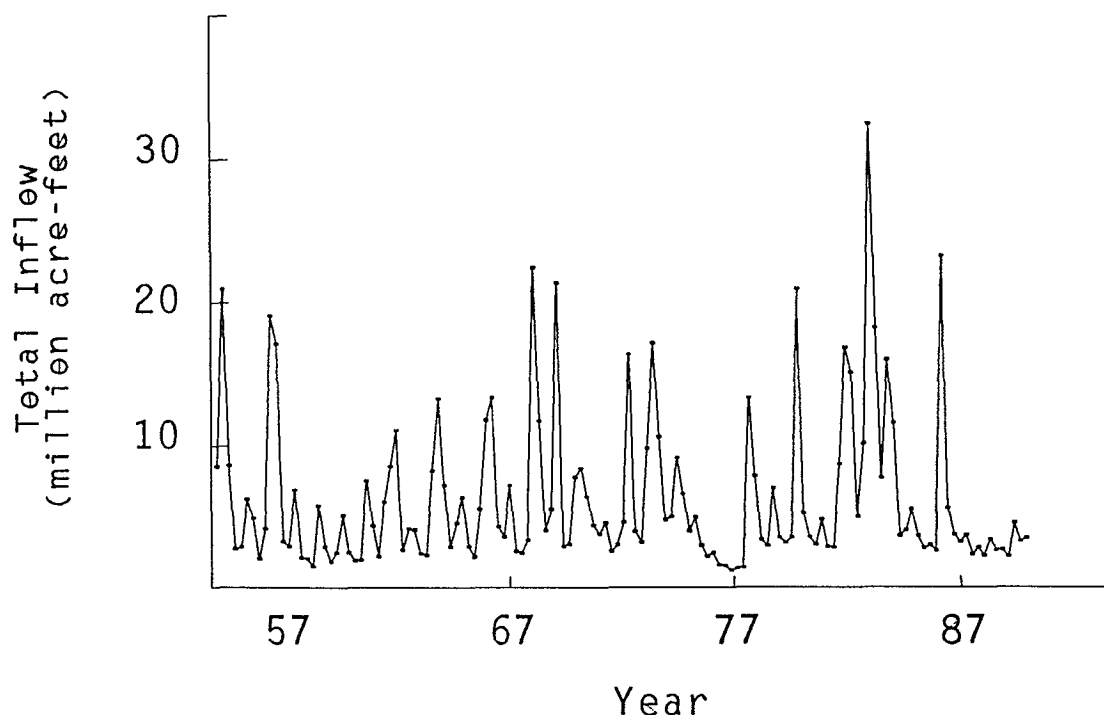


Figure 2 Quarterly inflows (in millions of acre-feet) into the estuary, estimated by the DAYFLOW model.

Diversion of inflowing water can alter all the cited effects of outflow. Water is retained and diverted by numerous channels and reservoirs on tributaries to the estuary, and these diversions account for about 30% of what is calculated to be the Delta's mean annual unimpaired flow. Agricultural diversions within the Delta claim about 1 million acre-feet of Delta inflow. These agricultural diversions are largely unscreened and are probably a major cause of larval and juvenile fish mortality. The greatest recent change in hydrodynamics of the Delta is associated with diversion of water from the Delta. The rate of these diversions has been increasing rapidly over the last 20 years and now takes as much as 60% of the inflowing water (Figure 3). The State Water Project and the federal Central Valley Project together comprise one of the largest water diversion projects in the world. In addition to simply altering the effective outflow downstream, diversion can alter the direction of net flow; opening of the cross-delta channel transports water of the Sacramento River through

the lower reaches of the Mokelumne to supply the state and federal water projects. Low outflow, when combined with high rates of diversion results in a net movement of Sacramento River water and water from Suisun Bay up the lower San Joaquin River channels. Diversions have intensified and broadened their impacts on flows within the Delta in the last few years. In water year 1987-1988 more water was exported than flowed into the Bay. This export of water from the Delta has been the largest change in water use patterns over the last 20 years and has coincided with declines of fish abundance. One purpose of this study is to identify which species appear most sensitive to the myriad impacts of diversion.

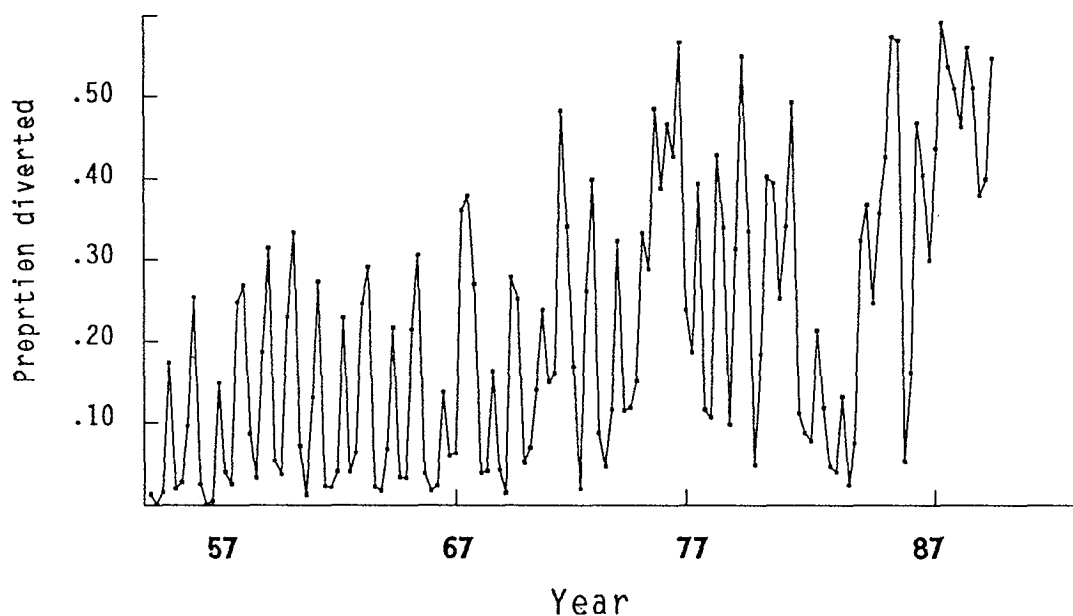


Figure 3 Quarterly proportion of delta inflow exported by State Water Project and Central Valley Project Pumps, from the DAYFLOW model.

Long-term trends in outflow have been the subject of several analyses and vigorous debate. The amount of fresh water entering the Bay is 50-60 % less than expected in the absence of upstream development and Delta diversions (Meyer and Davoren 1981; Nichols et al. 1986; Rozengurt et al. 1987; disputed by Fox et al. 1990). Operation of diversions and upstream dams have smoothed the annual pattern of outflow so that the summer and fall flows are much higher than in the past.

A period of very low precipitation in the earliest years recorded (1921-1935) and a shift toward precipitation falling as rain rather than snow results in an increasing trend in precipitation in the watershed over the period of record. Development of water projects has led to decreased Delta inflows in the late fall, winter, and spring. Some investigators have

argued that increasing supplies have outpaced demand and that Delta outflows have actually increased (Fox et al. 1990). However, mean monthly salinities in the Bay have risen in a pattern in close agreement with calculated declines in Delta outflow (Peterson et al. 1989).

Most analyses of freshwater inflow to San Francisco Bay have concentrated on the period since the large-scale diversions became active. The setting of annual entitlements of water to contractors by the state, despite the intrinsic high variability in the amount of water available in a given year, has resulted in an amplification of frequency and degree of drought conditions in the Bay (Rozengurt et al. 1987). The annual fluctuations may not be entirely unpredictable; between 1921 and 1978 inflowing water to the Delta shows evidence of 14-year cycles which have been found for other large drainages (Rozengurt et al. 1987). Proposed increases in water diversion in the future will continue to have their greatest effect on spring outflows, when most migrating or spawning in the Delta and Bay occurs. Currently mean annual spring diversion rates are around 60% and can be expected to rise to approximately 86% in future dry years. Average annual reductions in outflow can be expected to rise from 48 to 59%, and the modification of outflow can be expected to decrease the frequency of flushing flows (Williams and Fishbain 1987). These high diversion rates do not simply intensify the effects of normal droughts, they produce extended periods of anomalous flow patterns in the Delta.

Long-term records of precipitation in California from the analysis of tree rings show that the 20th century has been a period of exceptionally high rainfall compared to the three preceding centuries (Fritts and Gordon 1980; Figure 4). There seems to be no reason not to expect a return to the earlier rainfall patterns.

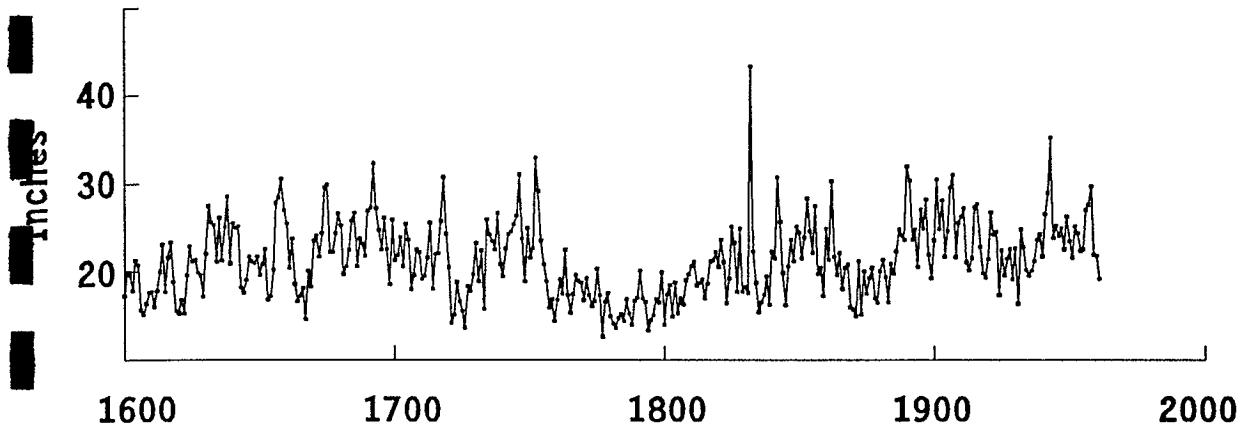


Figure 4 State-wide precipitation index for the period 1600-1960 based on analyses of tree rings.

Water diversion takes very small proportions of Delta inflow in wetter years; the recent high proportions are a result of a long drought period during a time of high diversion rates. The simple exacerbation of drought effects by water diversions and the changes in net flow direction, which can only be caused by diversions, are a principal point of interest in examining the trends in abundance for fishes of the estuary. However, consistent year-round data on fish abundances are only available for the last 10 years, so it is difficult to assess how the populations may have behaved in earlier drought years.

2.4 Pollutants

Changes in pollutant loads into the system will affect species in relation to three characteristics: the degree to which they are exposed to pollutants, their sensitivity to a given pollutant, and their trophic patterns in regard to bioaccumulation of pollutants. The effects of pollution in San Francisco Bay is the subject of another Status and Trends Report and will not be addressed in depth here. The major pollutants affecting aquatic resources in the Bay are petroleum based, including polychlorinated biphenyls (PCBs). Fish in aquaria are used to monitor the effects of outflows from sources such as refineries, but little work has been done to assess the impact of such pollutants on free-ranging populations in the Bay. PCBs have been shown to be at high levels in starry flounder collected from San Pablo and Central Bays and these fish show decreased reproductive abilities (Spies et al. 1988; 1990). It is difficult to determine the contribution of pollution load to the decline of this population (see section on starry flounder).

Benthic invertebrates are exposed to a wide variety of pollutants with effects ranging from the elimination of shellfisheries in the South Bay in earlier years (Nichols and Pamatmat

1988) to chronic stresses on shellfish of South and Suisun bays in recent years (Luoma and Phillips 1988).

Trace elements of particular concern in the Estuary include selenium (Johns et al. 1988; Cutter 1989), copper, cadmium and chromium (Luoma and Phillips 1988; Luoma et al. 1990). The effects of trace element contamination on higher trophic levels have been little studied; large-scale estimates of the impacts of such toxics on ecological processes in the Estuary are complicated by the complex distribution of 'hot spots' (areas of high concentration) in both time and space.

Different heavy metals enter the food web of the Estuary by different paths. Although selenium is a well-known contaminant in agricultural drainage of the San Joaquin Valley most of the high concentration of selenium, which has been shown to be correlated with condition (weight of flesh/shell length) of *Corbicula fluminea*, appears to come from human activity adjacent to the Bay (Cutter 1989). Likewise, chromium concentrations in Suisun Bay can largely be attributed to discharges from a local steel plant (Luoma et al. 1990). On the other hand copper transport into the Bay appears to be via high riverine flows (Luoma et al. 1990). In South Bay copper and cadmium are at similarly high concentrations in some areas but they appear to be tied to concentrations of salinity, organic carbon, or suspended particles (Luoma and Phillips 1988). Some concentrations of heavy metals in the tissues of animals of South Bay and Suisun Bay are quite high. Concentrations this high have been shown to affect growth and reproduction of clams in laboratory experiments. These gradients of low 'condition' and high trace metal concentration suggest that there is a likely effect of metals on bay aquatic resources, there is insufficient data to assess the impact on population sizes of benthos or on higher trophic levels.

Other sorts of pollution in the Bay that particularly affect aquatic resources include thermal plumes, primarily those from the PG&E plants in Suisun Bay and in South Bay. Thermal plumes affect aquatic resources in a variety of ways. The warm water outfalls into Suisun Bay provide temporary refuges for threadfin shad washed down from the Delta at the start of the wet season. On the other hand, warmer water can be an additional stress on fishes returned to the Bay from the fish recovery operations at Tracy. The restricted geographical range of thermal pollution limits its effect on aquatic resources, but the location of the outfalls into regions used for spawning by smelt and herring have the potential of affecting those species disproportionately. Some species are apparently drawn to the warmer waters nearer thermal outlets and may suffer disproportionately when those outlets fluctuate.

Principal pollutants in the Delta are the agricultural chemicals and their derivatives that are heavily used throughout the Central Valley. Recent concerns for pollutants in Delta waters have centered on trihalomethanes (THMs) in drinking water taken from the Delta, but the effects on aquatic resources of such carcinogens are unlikely to be a problem. The switch to short-stem rice by Sacramento Valley rice farmers was accompanied by increased use of pesticides and runoff from these waters may contribute to reproductive difficulties of striped bass (see section on striped bass).

2.5 Waterway modification

The earliest, and probably most profound, cause of change in aquatic habitat in the estuary was the introduction of European methods of agriculture into the Central Valley. Diking the rivers and clearing riparian vegetation began to change the lower parts of the valley from seasonal freshwater marsh to dry cropland. California has few natural lakes, and the two Delta species that were probably most lacustrine in their habits are the two are now extinct in their native region: thicktail chub and Sacramento perch. Populations of Sacramento perch remain in isolated lakes outside their native range. Populations of the genus *Gila*, to which the chub belongs, show much evidence of morphological specialization to local conditions (Moyle 1976). Characteristics of the thicktail chub include a number of features indicative of life in still water. Both species were formerly very abundant; Sacramento perch and thicktail chub are among the most abundant fish remains in Patwin Indian middens (Schulz and Simons 1973) and Sacramento perch were commercially harvested in the early days of San Francisco.

2.5.1 Diking

Diking of islands in the Delta began on Merritt Island in 1852. Dikes were constructed of dredged materials from the river or from the interior of the island. The dikes consisted of the river sediments, easily degraded peaty soils, or a combination of both. Such diking led to weak dikes, depressed island interiors, and deeper, more U-shaped channels in the river. Water flows more quickly in dredged channels and the vertical walls are easily eroded. Early efforts to bolster the dikes relied on simply widening them so that erosion took longer.

A secondary effect of diking was to change river habitats and primary productivity. Restriction of water to channels increased water velocity and lead to decreased residence times of water in the estuary and less time for phytoplankton to grow. The transformation of vast areas of freshwater marsh into cropland effectively eliminated the contribution of marsh productivity to downstream food chains. Approximately 10% of the Delta is now aquatic habitat, and 70% of that is deep, openwater habitat (USACE 1979) leaving less than 3% in a state similar to the majority of the Delta habitat 150 years ago. Channelization removed the shallow margins of most river channels and prevented the growth of benthic algae. Long residence times may have limited productivity within the Delta before diking, diversions, and dredging began. During low flow, summertime conditions high concentrations of phytoplankton may have blocked light penetration to most of the water column with a consequent decline in productivity. Shortened residence times appear likely to have reduced productivity within the Delta for most of the period of development, but an accurate model of productivity processes within the Delta has yet to be developed.

Diking has exerted a growing impact on the Delta since 1852. Reinforcing levee banks with rock revetments ("rip-rapping") and bringing publicly owned levees into conformance with federal guidelines of the U.S. Army Corps of Engineers has greatly reduced the incidence of levee failure. Only two inundated islands are today unreclaimed — Big Break on

Sherman Island in the western Delta and Frank's Tract (formerly Mildred Island) in the central Delta. Due to subsidence, soil oxidation, and loss of soil by plowing and exportation, the central portions of many islands are 20' or more below the level of the surrounding water. Thus, inundation would not restore the lost shallow habitats. Intentional inundation for temporary water storage provides a possible use for these islands that would greatly reduce their rate of subsidence and would reduce the problem of levee maintenance (Jones and Stokes 1990).

Diking and agriculture affected surviving fish species of the Delta in several ways. The following description of effects relies on the reproductive and trophic studies summarized in Wang (1986) and Moyle (1976). Sacramento splittail, Sacramento blackfish, and perhaps longfin and Delta smelt, require submerged vegetation for spawning; the removal of marshlands removed most of their potential spawning habitat. Prickly sculpin lay their eggs in chambers among the roots of emergent vegetation; they similarly suffered a decline in spawning habitat. Young fishes of all species suffered a massive reduction in the shallow habitats most of them use to escape predation. Tule perch, as consumers of the invertebrates living on emergent vegetation, lost much of their foraging area. Splittail today can be found foraging, as well as spawning, in shallow, flooded areas (Moyle 1976), and it seems likely that they would have formerly used the island interiors.

2.5.2 Dredging

The first dikes were built from dredge spoils. Dredging activities gained momentum from the flooding that resulted from upstream hydraulic mining. Deep water ship channels were dredged so that inland cities could engage in port commerce; Stockton today still celebrates its status as the easternmost port in Northern California in its nickname of 'The Sunrise Port.' Dredging and dike building in the Delta changed the character of the habitat and doubtless caused major, but undocumented, shifts in the manner in which fishes used the Delta.

Direct effects of dredging on aquatic resources today are greatly reduced by the restricted number of sites at which dredged materials may be deposited and regulation of quantity and timing when spoils may be dumped. Direct entrainment by dredge operations does not seem to be an important effect on anadromous fishes (Larson and Mohl 1990; McGraw and Armstrong 1990). Dredge spoils have not been found at levels sufficient to cause death of fish (Segar 1990). Any limiting effect on fishing success would probably be due to either decreased feeding by fish so that they take bait less often or by temporary migration away from Central Bay when dredging discharge rates are high. Available data are inadequate for analysis.

The most significant impact of dredging on aquatic resources appears to be the resuspension and release of sediments and pollutants into the water column. However, separating the effects of original contaminations from resuspensions requires considerable more background information on the effects of pollutants on the aquatic life of the Bay than

has been gathered to date. The plume from dredge disposal at Alcatraz does not persist for long, but it is likely that much of the plume remains suspended and is moved away from the dump site by tides (Segar 1990). Because finer sediments stay suspended longer and show higher toxic contamination, even though turbidity itself may not be at levels sufficient to harm fish, there is danger of toxic effects on fish (Segar 1990).

The effects of dredging and dredge disposal are expected to lessen in the near future (Hanson and Walton 1990). The San Francisco Bay Regional Water Quality Control Board has called for a ban on aquatic disposal of dredged material from all new projects in the bay and has established limits on the amount of material from maintenance dredging permitted at each disposal site. Finally, the board required that dredging activities be restricted in area and time to minimize effects on other beneficial uses of San Francisco Bay; specifically addressed were the needs of Pacific herring, striped bass, and king salmon.

2.6 Mining and siltation

Almost concurrent with the first diking of Delta islands was the advent of hydraulic gold mining in the Sierras. After the 1847 discovery of gold near a tributary of the American River, mining rapidly progressed from simple panning or sluice boxes in the stream to the use of high pressure hoses and large-bore water cannons to wash down much of the hillside. Miners constructed elaborate water systems to feed their operations, and in the 1880s hydraulic mining rerouted and used approximately 740 million cubic meters of water each year (Hagwood 1976). By way of comparison, average delta inflow is approximately 18 billion cubic meters, and the current water diversions export about 6 billion cubic meters.

The main impact of hydraulic mining on downstream sites was the introduction and transport of large quantities of silt. Siltation of river channels raised the bottom of the Sacramento River by 6 m and led to extensive flooding of the rapidly growing city of Sacramento. Of the 1.15 billion cubic meters of extra sediment estimated to have been brought into the Sacramento-San Joaquin Estuary, 155 million are estimated to have settled in Suisun Bay, 436 million in San Pablo Bay, and 249 million in South and Central bays; these volumes translate to new layers of sediment measuring 1 m in Suisun Bay, 0.8 m in San Pablo Bay and 0.2 m in South and Central Bays (Gilbert 1917). Hydraulic mining was banned in 1884 but the silt added to tributaries may have continued to affect water quality in the estuary until as late as the 1980s (D. Ball USBR, pers. comm.).

The effects of mining on the aquatic resources of the estuary were undocumented but undoubtedly devastating. Siltation and dewatering of spawning streams must have particularly reduced salmonid recruitment.

2.7 Introduction of species

Most changes in the estuary have been sudden changes of state rather than linear trends over years. For aquatic resources this has been most noticeable through the introduction of

non-native species. Populations of introduced species have either mushroomed or collapsed. As with most introduced species (Herbold and Moyle 1986), successful introductions into the Sacramento-San Joaquin estuary often have followed major changes in the physical structure of the rivers and estuary by humans. The siltation of the rivers by hydraulic mining and the subsequent success of striped bass and American shad typify this process. The failure of several early attempts to introduce channel catfish and their sudden explosion after Shasta Dam stabilized salinity and provided more consistent year-round flows in the rivers and the Delta provides another example (Herbold and Moyle 1989). Although the particular habitat change responsible that permitted the establishment of a particular exotic species into the Delta can only be the subject of speculation, the general observation that introduced species almost always follow habitat alteration appears to be as true in the Estuary as it is for the rest of the world (Elton 1958; Herbold and Moyle 1986; Fox and Fox 1986).

Justifications for introducing species frequently refer to 'vacant niches' in the environment, but this idea can be refuted either logically (most ecological definitions of 'niche' cannot be used in any 'vacant' sense) or through experience gained of hundreds of documented introductions throughout the world (Herbold and Moyle 1986). In looking at the effects on native species it is seldom possible to separate the effects of invading species from the effects of the habitat alteration that gave the exotics their chance. The difficulties are exacerbated by the scarcity of ecological information that is available to assess the effects of introduced species and of habitat modification prior to the mid 1960s. Early introductions of species, including striped bass, American shad, and carp, were often authorized or performed by governmental agencies. Most recent introductions have been unintentional.

As part of the massive effort to cash in on the gold rush by giving miners something to buy in the restaurants of San Francisco, the first planting of foreign species in San Francisco Bay may have been the Mexican oyster, *Ostrea chilensis* (Skinner 1962). Shiploads of oysters sailed north but many oysters died on route and the business never prospered. Following the gold rush came the transcontinental railway, which provided a means to transport live animals from the east coast. The first special ore cars to bring animals from the east contained American oysters and many of their symbionts and predators. Unlike the Mexican oysters, American oysters were laid into beds in the Bay and became a part of the benthic community. It is impossible to say for many invertebrate species, particularly fish parasites, whether they are native to California or were early, unintentional imports. The native California oyster (*Ostrea lurida*) was initially so abundant that their crushed, windrowed shells produced a "white glistening beach that extends from San Mateo for a dozen or more miles southward" (Townsend 1893). The accumulated native oyster shells supported a long-lived local cement company. Unfortunately, the flesh of the native oyster was disdained by the newly arrived Californians (Nichols and Pamatmat 1988), so that after the native oysters had been harvested from their beds they were replaced with plantings of American oysters. The native species was "thrust into the background" (Bonnot 1935).

Frog legs were another San Franciscan delicacy that resulted in new species introductions. After hunting drove the native red-legged frog (*Rana aurora*) to the point

where they could not be profitably harvested, bullfrogs (*Rana catesbeiana*) were introduced (Jennings and Hayes 1985). Overharvest of female red-legged frogs, combined with predation by the much larger bullfrog and introduced fish, are believed to have exterminated the Central Valley population of red-legged frogs (Hayes and Jennings 1986).

Crayfish were another food species whose distribution was changed as a result of human activities. Three species of crayfish were introduced: the signal crayfish, *Pacifastacus leniusculus* var. *leniusculus*, the red swamp crayfish, *Procambarus clarki*, and a species with the common name *Orconectes virilis*. No crayfish are reported in Native American middens of the Central Valley Patwin tribe (Schulz and Simmons 1973), but a crayfish (*P. nigriscens*) was described from specimens collected in tributaries to the South Bay. It is now extinct. Signal crayfish support a large fishery in the Delta (Kimsey et al. 1982) and the red swamp crayfish is widely distributed in the drainage. *Orconectes virilis* is a threat to the survival of native crayfish in the upper Sacramento Valley.

Following the completion of the transcontinental railway in 1869, young American shad were transported from New York beginning in 1871. Common carp came into the state from Japan in 1872 through the efforts of an early aquaculturist. Trans-Pacific shipping as a means of species introduction began in 1877 when the California Fish Commission imported 88 carp from Japan. In 1874 a flood of new species followed completion of the transcontinental railway, including largemouth bass and several species of catfish and bullhead. Striped bass were introduced at Martinez in 1879 from a shipment from New Jersey (Skinner 1962).

The introduction of oysters, bullfrogs, crayfish, striped bass, and American shad was only the beginning of a long series of introductions that continues to this day. In the 19th century and the first half of this century, most introductions either were made deliberately in efforts to "improve" the local fauna from the perspective of western culture or they were made accidentally, as species hitched rides in containers with the authorized species or came attached to ships. As a result, more than half the fishes in the Delta are non-native species (Harbold and Moyle 1989), and most of the benthos of the Bay is made up of exotic species (Carlton 1979; Nichols and Pamatmat 1988). New species are continuing to arrive in the Estuary, especially in ballast water of ships, as demonstrated by the recent destructive invasion of the Asian clam, *Potamocorbula amurensis* (Carlton et al. 1990). The presence of so many recently established species in the Estuary, combined with continual arrival of new species, contributes greatly to the instability of the Estuary's biotic communities and increases the difficulty of managing it to favor desired species.

2.8 Exploitation

Many of the molluscs, crustaceans, and fishes of the Estuary have been heavily harvested by humans (Skinner 1962). There is little doubt that overexploitation of species such as chinook salmon, white sturgeon, softshell clam, and crangonid shrimps contributed to their declines in the early part of this century. The sturgeon and shrimp populations in fact showed dramatic recoveries once commercial fisheries were eliminated or reduced.

However, as the accounts of individual species show, overharvest has played, at best, a minor role in the long-term declines of the estuary's aquatic resources.

Major Factors Expected to Affect Aquatic Resources

3.1 Global warming

Global warming is the long-term trend most likely to have the greatest impact on aquatic resources of San Francisco Bay. The debate surrounding the evidence for global warming and the estimates of rates and degrees of warming have attracted wide public interest. Academic, federal, state, and private studies have generally concluded that global warming is at least very likely and that certain aspects may be unavoidable (USEPA 1983, 1988; California Energy Commission 1989; Gleick and Maurer 1990; Regier et al. 1990). Although the recent extreme weather conditions in California may have little to do with global warming, their effects on aquatic resources of the Bay and Delta are similar to some of the effects expected to be associated with a global warming trend.

Global warming is apt to alter ecosystems via three mechanisms (Regier et al. 1990): direct alteration of the physical environment of animals, changes in the operation of physical and biotic linkages within communities, and alterations in the physical environment as a result of human response to the effects of global warming. The first mechanism is probably more important for terrestrial systems than aquatic ones, due to the heat-buffering capacity of water. One possible direct effect of increased temperature is that of decreased availabilities of oxygen in warmer waters; this has been proposed as a mechanism for explaining the variable success in introducing striped bass (Coutant 1981, 1990). Thus, global warming may pose an added difficulty for recovery efforts for the striped bass fishery in San Francisco Bay. The degree of human manipulation of the physical habitat of San Francisco Bay makes it difficult to separate the effects of humans from human response to global warming from ecosystem mechanisms.

A second major effect of global warming on the aquatic life of the Bay will be reduction or loss of shallow water and intertidal habitats as sea level rises (Gleick and Maurer 1990). Sea level is estimated to rise between 13 cm and 55 mm by the year 2025, and by 24 cm to 1.17 m by the year 2050 (USEPA 1983). Unambiguous effects of rising sea level are not expected to be felt until 2020 when rates of rise are expected to increase from this century's average of 1-1.5 mm/year to probable rates of 3 to 15 mm/year in the next century (USEPA 1983). Intertidal habitats of the South Bay that lie between present mean low water and the lower limit of urban development are almost certain to be lost with any appreciable sea level rise, as they are apt to be converted to dikes and other flood control structures. Wetland habitats around San Pablo and Suisun bays may be lost entirely due to flood control, but the reduced intensity of urban development in these areas may permit some to become intertidal habitats. Passive sea level rise will certainly cause problems, but political pressure to isolate or convert wetlands by dikes will be amplified by the greater incidence of large storms that will accompany global warming trends (Gleick and Maurer 1990). These storms are expected to show as much as a tenfold increase in frequency under a global warming scenario of only a 15 mm rise in sea level.

Sea level rises and global warming will entail changes in the mean salinity and in the pattern of annual changes in salinity that characterize the northern reaches of the Bay. Sea level rises will push salt water further upstream, and this effect will move mean isohaline profiles 15 km upstream; increased storms will provide more freshwater outflows for a net effective upstream migration of salinity profiles of only 10 km (Williams 1989). Direct effects of increased saltwater intrusion are expected to interact with substantial alterations in patterns of freshwater inflow. Rising sea levels are apt to lead to massive levee failures within the Delta. Agricultural practices within the Delta have reduced the levels within Delta islands by as much as 10 m, so that levee failures will serve to transform the Delta into an inland arm of the Bay rather than back to its primitive state as a marsh. Sediments would tend to accumulate in the upper bay and Delta as the ratio of seawater inflow to freshwater outflow shifts toward marine influences. Stronger and more frequent wintertime storms will lead to increased erosion of the perimeter of the lower bay and make these sediments available to landward-flowing bottom currents. Contrarily, increased storm frequency and severity will increase transport of sediment out of the Delta during the winter. Human responses to these climatic and environmental changes could include construction of a wide variety of protective structures, probably at Carquinez Straits or in the western Delta. These massive and poorly quantifiable changes in aquatic habitats of San Francisco Bay and Delta will have similarly massive and poorly quantifiable effects on aquatic resources.

The effects of a global warming pattern on precipitation in California are unpredictable, except that warmer temperatures will cause a greater percentage of precipitation to fall as rain rather than snow (California Energy Commission 1989). The more rapid runoff of rainwater will tend to restore the seasonality of outflow through the estuary. Even if precipitation stays the same or increases, a higher percentage of winter runoff will have to be released for flood protection and the smaller snowpack will reduce the amount available for release in spring and summer. A 3° C warming would reduce the area of the Sierra snowpack by 54%, and reduce total unimpaired runoff through the estuary from April to July by 33% (California Energy Commission 1989).

3.2 Water Development

A continued trend with the potential to have great impacts on aquatic resources of the Estuary is further water development in the Central Valley. Possible developments include:

1. increased water storage on tributary streams by such proposed projects as Auburn Dam or the enlargement of Shasta Dam;
2. more rapid transport of water through or around the Delta by deepening of channels or construction of facilities like the New Hope Cross Channel;
3. increased storage downstream, as with Los Vaqueros and Los Baños Grandes reservoirs, to capture more winter and spring runoff;
4. establishment of temporary storage facilities within the Delta to provide a holding area for water to be released after river flows decline, as in the proposed Delta Wetlands project.

Each of these types of development serves to give greater control of water through the delta so that a larger and more constant supply of water is available for diversion. Thus, each share effects that reduce seasonality and flow patterns in the estuary, but each also has different secondary effects on aquatic resources. Secondary effects due to increased stream storage will include further declines of anadromous species. The increased dominance of the fall run chinook salmon relative to other salmon runs is partially an effect of the cool water discharges from Shasta Dam that provide appropriate temperatures for spawning below the dam during August and September. Further water development is likely to accelerate the declines of other runs. Similarly, the migration of first-time spawning American shad up tributary streams is largely triggered by the amounts of water entering the mainstem from the tributaries (Daniel 1989, cited in California Energy Commission 1989). Further damming or diversion on the tributary streams is apt to reduce their ability to sustain runs of American shad.

3.3 Effects of likely future changes on aquatic resources

Based on the forgoing we expect the future of aquatic resources of San Francisco Bay and delta to be most affected by four processes:

1. **Increasing rates of diversion will reduce the amount of water flowing into and through the Estuary.** This will produce more frequent drought conditions in the Bay by making normal years have the outflows expected of dry years and dry years have the outflows of critical years. Even if diversion rates are held at current levels, the amplification of the effects of occasional drought conditions is likely to produce further shifts in aquatic resources of the Bay and Delta. The drought of 1976-77 coincides with several major shifts in the abundance of aquatic resources and the drought of the late 1980s coincides with further sharp changes in the abundance and species composition of aquatic communities of the upper Bay.
2. **Increasing global temperature will increase the amount of salt water entering the Bay, relative to fresh water.** Total volume of water in the Bay will also increase and lead to unforeseeable changes in patterns of land use and reclamation. Increased sea level will also reduce the amount of fresh water which can be exported from the Delta by the mechanisms currently in place and will probably result in unpredictable changes in water export procedures.
3. **Land use patterns will change with unpredictable effects on the water available for aquatic resources.** Delta islands are apt to be flooded either deliberately or accidentally, which would decrease the number of unscreened diversions in the Delta, but increase the total amount of water diverted (if the islands are used for water storage) and would change flow patterns through the Delta. Salinization of soils, unacceptable levels of contaminants in drainage water, and other factors may result in large tracts of land being removed from irrigation which would increase the amount of water available for other purposes.
4. **Exotic species are likely to continue to invade the estuary.** If habitats are changed by any of the projected trends it will increase the likelihood of success for some of the

introduced species. The effects of the newly introduced copepods have begun to be understood in relation to other aquatic resources. The Asian clams have not been around long enough, particularly under wet year conditions, to estimate their impact on the future of the Bay. As in the past, it will be difficult to separate the effects of habitat alteration on the aquatic resources of the estuary from the effects of introduced species that are better able to use the altered habitats. The species which will invade are impossible to predict, but they are likely to continue to be species transported in ballast water.

3.4 Use of existing data to estimate effects of future trends

The drought of the last five years may have created conditions indicative of the permanent changes likely if San Francisco Bay changes toward a more ocean dominated system as a result of either global warming or decreased freshwater outflows. This assumption allows assessment of how each aquatic resource species responds to decreased outflows and increased marine intrusion, but it cannot encompass the effects expected from increased wintertime storms. The aquatic community of the Bay has been intensively studied only since about 1980, and the first five years provide examples of the strong annual variations in outflow that have typified the Estuary for much of its recent history while the second five years have been drier than average for almost all months. Changes in the abundance of each species within each year show several clear shifts from the more normal conditions of the early 1980s to the prolonged drought of the latter 1980s. The fact that many of these trends are sharp and parallel for species that use similar parts of the estuary suggests that, although the data span only ten years, they are sufficient to identify the dominant trends in the system. These trends are the subject of most of the rest of this report.

Aquatic Resources

1 Introduction

The aquatic resources of the Sacramento-San Joaquin Estuary can be grouped into two categories based on their relationship to human interests:

- species that are directly harvested by humans, or that support (or inhibit) the production of harvested species and
- species that are valued for their aesthetic or biological characteristics.

The membership of each group has shifted with the abundance and use of the species individually and with the perception of the species by different groups of people. For instance, the Sacramento splittail was harvested by Chinese-Americans, was considered a competitor with striped bass by striped bass anglers, and is now being considered for protection as a threatened species by the USFWS. The trend since the mid-1800s has been toward increasingly strict regulation of harvest, a shift from commercial to sport fisheries for most species, regulation or mitigation for factors shown to degrade fisheries, and attempts to protect endangered species.

Directly harvested species range from the dense beds of native oyster shells that supported cement manufacture for almost a hundred years (Skinner 1962) to the valuable commercial fisheries for salmon, Dungeness crab and herring roe, to the popular sport fisheries for striped bass, catfish, and sturgeon. All of the harvested species have undergone large fluctuations in their yields (and presumably in their populations) during the 150-year history of exploitation of the Bay.

The species that affect the food supply and health of harvested species were largely unstudied until the 1960s. General ecological knowledge, current understandings of the biological structure of the estuary, and records of conditions in prior times are the only clues in constructing the 'natural' status of the estuary or the steps it has passed through to get to its current state. Traditionally, aquatic biologists have distinguished between the food produced within the ecosystem being studied (autochthonous) and that carried in from other systems (allochthonous). This 'fixed carbon' may enter food chains of the Sacramento-San Joaquin estuary from five sources:

1. algae in the water of the estuary (phytoplankton),
2. algae growing on the bottom of the estuary at depths shallow enough to permit photosynthesis, at least during low tide (benthic algae),
3. algae and other plants of tidally inundated marshes,
4. fixed carbon in any form (plant or animal products, including non-living parts) carried in from upstream (riverine contributions), and
5. fixed carbon in any form (plant or animal products, including non-living parts) carried in from the ocean (oceanic contributions)

The determination of where the fixed carbon comes from and how much of it actually enters the food web of the estuary is fundamental to estimating the quantity of animal material the estuary can support.

The quantity of fixed carbon available to animals can be estimated from the sum of each of the component sources minus the potential losses to various 'sinks.' Outflow and diversion, migratory animals, and loss to sediments are some of the ways fixed carbon can be lost. Carbon consumed by animals which die in the estuary is not lost except for the amount broken down by respiration. The respiratory rate of the animals involved and the number of trophic levels in the food chain can affect the standing crop of animal biomass. Thus, the carbon budget sets a limit on possible biomass, but the structure of the animal community controls the size of the standing crop.

Knowledge of this 'carbon budget,' however, can give no indication of which animal species might benefit. The species composition of all trophic levels in the estuary has repeatedly changed as habitats have been altered, species have been decimated and new species have invaded. The different habitats in the estuary appear to have supported separate ecological communities, even though the abundance and species compositions have changed. By identifying the sorts of species characteristic of each part of the estuary we hope to suggest which are likely to receive a larger share of the carbon budget in the future.

Since the 1960s, massive efforts have aimed at increasing water quality and reducing pollution of the Bay. Coincident with this has been a growing appreciation of the aesthetic and biological value of aquatic resources of the Bay and Delta. Specialized, private organizations such as Save the Bay and The Bay Institute reflect a growing appreciation by the public of the natural values of the Bay. Broader scale environmental groups, such as the Environmental Defense Fund have increased their involvement in attempts to safeguard aquatic resources of the Bay for, largely, non-consumptive use. The activities of these groups have often focussed on the continuing decline of native fishes as well as the declines of various harvested species.

Species that have particularly drawn the attention of people working to preserve the aesthetic or ecological values of the estuary have included the spring and winter runs of chinook salmon, the Delta and longfin smelts, and the Sacramento splittail (Moyle et al. 1989). Curiously, all these species have supported fisheries in the past but have declined to such low values they are no longer economically important. Instead they are appreciated for their heritage values and as indicators of ecosystem health.

The aquatic resources of the Estuary include much more than endangered species and species of economic importance. They include entire trophic webs from bacteria and algae through fish, birds, and mammals. In this report we present the status and trends in a traditional hierarchical fashion from bacteria, algae, zooplankton, and benthos to fish and fish assemblages. The emphasis on fish largely reflects the amount of information available.

Birds, mammals, and some additional invertebrates are covered in the Wildlife Status and Trends Report.

4.2 Primary Producers (for description of productivity patterns see Appendix A)

4.2.1 Bacteria

Bacteria play an essential role in both the food webs and the biogeochemical cycles of estuaries. On a functional basis, several groups can be recognized. *Heterotrophic* bacteria are dependent on organic material for their carbon and energy, whether these materials are produced within the estuary by primary producers such as phytoplankton or are introduced into the estuary by, for example, river flows, waste water, or tidal marsh export. *Aerobic* heterotrophs require oxygen for their metabolism and are found in the water column and surface sediments. *Anaerobic* heterotrophs live in anoxic sediments and oxygen-free microzones surrounding detrital particles in the water column. These anaerobes utilize nitrate and sulfate as a source of oxygen, producing reduced substances such as methane, ammonium, and hydrogen sulfide. One of these anaerobic pathways involves the formation of nitrogen gas, an important process known as denitrification. *Chemoautotrophic* bacteria, in turn, use these reduced products as an energy source and carbon dioxide as their carbon source. As a result of their metabolism, some of the reduced substrates they depend on for energy are oxidized back into nitrates and sulfates. Finally, *photoautotrophic* bacteria use light as their energy source and carbon dioxide as their carbon source; in contrast to plants, however, these bacteria use reduced compounds instead of water as a hydrogen donor.

4.2.2 Protozoans

The Protozoa are single-celled organisms that are generally heterotrophic, subsisting on organic material, although some may derive supplemental energy from photosynthesis. Most are particle-feeders that consume bacteria, algae, particulate organic matter, other protozoans, and even smaller metazoans. The common mode of reproduction is mitosis and binary fission. Aside from those forms that are internal parasites of other animals, most protozoans in temperate coastal areas are ciliates or flagellates. Ciliates are usually found in conjunction with high concentrations of decaying organic matter—for example, in or near the sediments—but one group, the Tintinnidae, is common to the pelagic zone. The genus *Tintinnopsis*, for example, is characteristic of shallow coastal waters and has at times been observed at high concentrations throughout the Bay and in the western Delta (Sitts and Knight 1979; Ambler et al. 1985).

4.2.3 Algae

4.2.3.1 Phytoplankton

Phytoplankton are the small, usually microscopic, plants that occur in every water body. They are primarily photosynthetic, but some may supplement energy needs by assimilating dissolved organic compounds and even, in some cases, detrital particles or other organisms. Phytoplankton are extremely diverse in terms of taxonomic status, habit and life cycle, and this diversity is no less characteristic of estuarine phytoplankton communities.

The lower reaches of estuaries are usually dominated by diatoms; dinoflagellates are less abundant but can be important at times. Smaller flagellated forms, such as cryptomonads, can also be numerous. Neritic diatom species from adjacent coastal waters penetrate estuaries to varying degrees, depending on their capacity to withstand reduced salinities. Upstream, estuarine species that are of minor importance in fresh or marine waters may predominate. Further upstream, the estuarine communities give way to freshwater assemblages.

The major algal group in estuaries is the class Bacillariophyceae, the *diatoms*. Diatoms are usually solitary, although filamentous and colonial forms also occur. Their cell wall, or *frustule*, is composed of silica with an organic coating. Their pigments are both carotenoids and fucoxanthin, which give most of them a golden-brown color. Planktonic species may be *holoplanktonic*—able to complete their life cycle independent of the bottom; *meroplanktonic*—pelagic for only a short portion of their life cycle; or *tychopelagic*—usually attached but sometimes swept into the water column. Thus, certain species may be collected from the water column, from sediments, or off of some substrate. Planktonic cells often have morphological adaptations such as flattening or spines that slow their sinking rates.

A second important group is the class Dinophyceae, the *dinoflagellates*. These are unicellular organisms with two flagella that are common in estuarine waters, although not so prevalent as diatoms. They are usually photosynthetic, but consumption of dissolved and particulate organic matter is a well-developed mode of nutrition in some species. Some dinoflagellates are "armored" with thick *thecal* plates that may form conspicuous wing-like projections. Several marine dinoflagellates are bioluminescent. Dinoflagellates also produce blooms or "red tides" in which the waters are colored by the high concentration of cells. Some of these blooms are associated with toxin production and may be responsible for fish or invertebrate kills. Other blooms may not kill many marine organisms, but the toxin can become concentrated in shellfish and pose a hazard to humans consuming the shellfish.

Small flagellated algae form a third important group in the estuary. These are primarily members of the Cryptophyceae, the *cryptomonads*. Cryptomonads have asymmetric, flattened cells with two flagella. A wide range of pigmentation can be found in cryptomonads, including red, blue and green. Species occur from freshwater to marine habitats, and some of them are tolerant of quite wide salinity fluctuations. Although most are photosynthetic, some can feed on dissolved organic matter. In many environments, cryptomonads "fill in" algal

communities between bloom periods, although they are usually not capable of forming massive blooms themselves—probably because of susceptibility to grazing.

4.2.3.2 Benthic microalgae

Benthic microalgae—known also as the *microphytobenthos*—occur primarily in the upper millimeter or so of sediments, although they can be found alive at greater depths. The benthic microalgal flora is a diverse assemblage of diatoms, blue-green algae, and flagellates, usually dominated by pennate diatoms. Photosynthesis is the primary nutritional mode. Benthic microalgae are much less sensitive to high light intensities than are phytoplankton, so that exposure to full sunlight in intertidal areas is generally not harmful. Many benthic diatoms have an endogenous circadian rhythm in which they migrate vertically through the sediments; this migration enables them, to some extent, to control exposure to light. These grazing algae often leave a trail of mucus, which may serve as nutritional support for other microorganisms. The algae themselves are ingested and assimilated by many epifaunal and benthic deposit feeders. Typical benthic microalgae include species of *Navicula*, *Nitzschia*, *Porosigma*, and *Cylindrotheca*. Meroplanktonic taxa such as *Melosira* are often found alongside these truly benthic forms.

Sediments in the San Francisco Estuary contain typical estuarine species such as *Nitzschia minimata* and *N. pusilla* in the South Bay shoals (Nichols and Thompson 1985a), as well as species characteristic of more saline and oligohaline environments in Central Bay and Suisun Bay, respectively. The distinction between benthic microalgae and phytoplankton is not always clear. In Suisun Bay, for example, phytoplankton such as *Thalassiosira decipiens* may accumulate on sediments as their bloom in the overlying water terminates. In the central delta, *Melosira granulata*, which has bloomed in the water almost every year since 1979, is also an important component of the benthos at times.

4.2.3.3 Macroalgae

The macroalgae—often known as seaweeds—are a diverse group of large algae. Estuaries are usually colonized by marine species, and freshwater species predominate only near the head. In the middle reaches of estuaries, there may be a few species confined to brackish water. Hard substrates usually support the greatest diversity of macroalgae. In San Francisco Bay, these are most common close to the Golden Gate. But even though diversity decreases away from the Golden Gate, the soft sediments of southern San Francisco, San Pablo, and Suisun bays, the biomass of individual species can still become substantial. Species diversity usually decreases upstream, with green algae (Chlorophyta) having the widest distribution within the estuary. The most common green macroalgae in estuaries include *Enteromorpha*, *Ulva*, *Ulothrix*, and *Ulva*, among others. The brown alga *Fucus* and the red alga *Polysiphonia* also have a wide distribution in estuaries.

Jones and West (1985) have reviewed the occurrence of macroalgae within the San Francisco Estuary. Over 160 species have been noted. As in other estuaries, the most common forms are green algae belonging to the genera *Enteromorpha*, *Ulva*, and

Cladophora, *Ulva* and *Enteromorpha* spp. can form extensive mats on estuarine mud flats. *Polysiphonia*, a common red alga in San Francisco Bay, also can form nuisance blooms.

4.2.4 Seagrasses

Seagrasses are marine angiosperms characteristic of tropical and temperate estuaries. Although there are a dozen or so higher plant genera that can function normally and complete their life cycles in saline waters, the most widely distributed dominant in temperate estuaries is *Zostera* or eelgrass. Seagrass beds may consist of only a few isolated plants or clumps of plants, or may be dense and extensive. Bottom morphology and sediment dynamics are critical in establishing the range and density of seagrass beds. Seagrasses often have significant quantities of attached epiphytes associated with them, and they can provide both food and cover to a number of crustacean and fish species.

4.3 Plankton communities

4.3.1 South Bay

In almost all water bodies, trophic relationships on the microscopic level can be quite complicated. In addition to the classic pathway, in which energy passes from primary producer (e.g. phytoplankton) to a macroscopic consumer (e.g. copepod), a number of other pathways have become recognized over the past few decades. Although these alternative trophic links in the San Francisco Estuary have not received much attention, they are almost certainly of importance. Some generalizations from studies in other estuaries are therefore in order. These microbial relationships are probably present throughout the Estuary.

In the water column, many kinds of organic matter are present. Although most of the living material in the Estuary's waters may be in the form of microalgae, large amounts of *detritus* -- dead organic matter -- are also present. Some of this material may have originated from extracellular products of photosynthesis or dead phytoplankton, but many other sources probably contribute as well (Appendix A). This detritus, depending on its form and size, may support higher organisms in several ways. In particulate form, some of it might be consumed directly by copepods, but much of it is probably processed by bacteria, which in turn may be consumed by protozoans. The work of Hollibaugh and Wong (pers. comm.) has shown that this "microbial loop" is quite active in certain parts of the Estuary. Planktonic aerobic heterotrophs appear to form part of an important food web pathway in the San Francisco Estuary. Production at times rivals and even exceeds phytoplankton production, reflecting the presence of alternative energy sources such as riverine inputs of organic matter (Hollibaugh and Wong, pers. comm. 1991). Much of this production may be passed on to bacterivorous zooplankton and zoobenthos.

Some of the smaller algae are probably consumed by protozoans as well. Small flagellated algae such as the cryptomonads are common in almost all parts of the estuary. Tintinnids can serve as an important trophic link between small phytoplankton ($< 10 \mu\text{m}$

acter) and metazoan zooplankton such as the estuarine copepod *Acartia* (Robertson 1983). As mentioned previously, *Tintinnopsis* can be common throughout the Bay and western areas of South Bay during spring and summer of certain years (Bain et al. 1968; Cloern 1984). Small flagellated protozoa are known to play a similar trophic role in many water bodies, but their significance in San Francisco Bay has not been delineated.

The presence of these microbial pathways is of the utmost importance. Each trophic link usually represents a substantial loss of energy to the system due to respiration. Unassimilated or excreted material has the opportunity to enter the food web again, but respiratory losses are a true sink. The proportion of production at one trophic level that is passed on to the next is highly variable, depending on the organisms and ecosystems in question, but it is not unusual to pass on only about 25%. As a consequence, the interposition of an extra trophic link can be equivalent to a four-fold drop in organic matter sources at the base of the food web. It is therefore important to focus on the food web structure, as well as the supply of energy to the base of the food web. Analyses are much further along with the latter issue (Appendix A) than the former. The lack of understanding of these microbial trophic relationships in the Estuary is a serious obstacle to understanding the ecosystem.

In San Francisco Bay, planktonic diatoms are usually the dominant algal form during winter blooms (Cloern 1984; Cole et al. 1986). In South Bay, dominant bloom species include *Cyclotella* spp., *Thalassiosira* spp., and *Skeletonema costatum*. Diatoms are often abundant at other times of the year, when small flagellated algae may predominate. They include the cryptomonads *Chroomonas* and *Cryptomonas*, as well as the green alga *Chlamydomonas*. In South Bay channels, bacterioplankton production can be a large fraction of zooplankton production, although the ratio is much less in shoal areas. During winter 1980, tintinnid protozoans—mostly *Tintinnopsis* spp. and *Eutintinnus* spp.—constituted only a few percent of the zooplankton biomass (Ambler et al. 1985). Rotifer biomass, primarily *Synchaeta* sp.—was less than 1% of the total. During summer 1980, protozoan and rotifer biomass was even less important. Limited experiments suggest that most of the bacterioplankton production is being grazed (Hollibaugh and Wong, pers. comm.). As adult copepods cannot readily feed on isolated bacteria, either most of the grazing occurs on floating detrital particles, unidentified bacteriovores are present, or the contribution of these protozoans, rotifers, and copepod nauplii to secondary production is much higher than suggested by their biomass. The dominant copepods of South and Central San Francisco Bay are *Acartia* spp. and *Oithona davisae*.

4.3.2 San Pablo Bay

Thalassiosira spp. were the major bloom taxa in San Pablo Bay in 1980 (Cole et al. 1986). *Skeletonema costatum* can also be a dominant. Various *Cyclotella* species dominated the post-bloom period, and *Melosira* spp., *Fragilaria crotonensis*, and *Amphora* spp. dominated before the bloom. Unlike South Bay, small flagellated cryptomonad and green alga did not appear to be important. Protozoan and rotifer biomass were also less important

than in South Bay, which may reflect the paucity of small algae. The diversity of both protozoans and rotifers increased, however. The tintinnid *Parafavella* and rotifer *Keratella* were observed in San Pablo channel samples, and the rotifer *Brachionus* in the Carquinez Strait channel. Bacterioplankton production also was a smaller proportion of phytoplankton production in San Pablo Bay, compared to South Bay, although still substantial (Hollibaugh and Wong, pers. comm. 1991). Larger zooplankton species include the copepods *Acartia* and *Eurytemora* in the dry and wet seasons, respectively.

4.3.3 Suisun Bay

Suisun Bay phytoplankton blooms were dominated by *Skeletonema costatum* and *Thalassiosira decipiens* in 1980 (Cole et al. 1986). *Melosira*, *Cyclotella*, and unidentified green algae were important at other times of the year. *Keratella* sp. was the dominant rotifer and *Tintinnopsis* sp. the dominant protozoan. Both rotifers and protozoans appeared to be unimportant in terms of biomass. Bacterioplankton production was comparable to that of San Pablo Bay. Larger zooplankton include *Eurytemora* and the recently introduced *Pseudodiaptomus*. In dry seasons *Acartia* usually invades, and in wet seasons the upstream copepods *Diaptomus* and *Cyclops* appear along with cladocerans such as *Bosmina* and *Diaphanosoma*.

4.3.4 Delta

Wintertime phytoplankton of the Delta are frequently dominated by cryptomonads (Ball 1975) or the diatom *Achnanthes* (California Department of Water Resources 1978-86a,b). However, these wintertime populations are usually at low densities, so the emphasis in the following discussion is on those species that dominate the productive period from spring to fall.

The distribution of species can be masked by their simultaneous growth periods. The 1984 peak in chlorophyll *a* (California Department of Water Resources 1985a) showed a maximum in the south central Delta with a more rapid decline toward the west and north than toward the south, suggesting a single bloom. In fact, this bloom varied in species composition as much as in density (California Department of Water Resources 1985a). In 1982 there was a similar situation (California Department of Water Resources 1983a) when three more-or-less simultaneous blooms, were responsible for the high June concentrations of chlorophyll *a* throughout the Delta. Because of the formation of transition zones, five different algal communities constituted this bloom (California Department of Water Resources 1983a). Small-scale discrepancies in timing of the peaks within these associations (California Department of Water Resources 1983a) suggested that they were controlled by different environmental factors. The different growth rates of the different species responsible for these blooms may be one of the largest stumbling blocks in developing a predictive model of delta phytoplankton (HydroQual 1984; Brown 1987).

4.3.4.1 Western and Central Delta

In the western and central Delta, prior to 1976, phytoplankton blooms were dominated by *Skeletonema potamos*, *Melosira granulata*, *Thalassiosira* spp., or *Cyclotella* spp. (Ball 1987). In May of 1976, however, a bloom of *Melosira granulata* occurred. Since that time, almost all large blooms have been due to *Melosira granulata*. The small cryptomonad flagellate *Chlamydomonas lacustris* is also widely distributed throughout much of the Delta.

4.3.4.2 Northern Delta

The northern Delta is dominated by the waters of the Sacramento River and associated Yuba Bypass and supports the lowest phytoplankton concentrations of the area. Water from the Sacramento River enters the Delta carrying chlorophyll *a* at concentrations seldom greater than 6 µg/L in the summer. During the winter, when water residence times, stratification, and temperature are least, chlorophyll *a* concentrations are frequently as low as 1 µg/L. As the water flows through the Delta to Green's Landing these concentrations are generally doubled. The low flows during the 1976-77 drought generated phytoplankton concentrations several times greater than these. High-flow years can prevent any measurable phytoplankton growth.

This area, like most of the Delta, is dominated by diatoms (Bacillariophyceae) but flagellates are occasionally abundant. Abundances peak in the spring, although in 1984 there was a wintertime peak because of *Asterionella* in January and *Cyclotella* in February. From 1969 to 1974 the dominant phytoplankton were *Thalassiosira*, *Cyclotella*, and *Melosira* (Ball 1977, Ball and Arthur 1979).

4.3.4.3 Southern Delta

The southern Delta is dominated by waters of the San Joaquin River. The San Joaquin is generally shallower, warmer, slower-flowing, and more nutrient-rich than the Sacramento and, so, has supported much greater concentrations of phytoplankton. Peak plankton abundances in the south Delta are regularly 10 times as dense as those in the rest of the Delta. Because of the recirculation of agricultural water through the San Joaquin Valley, the south Delta has higher conductivities than most of the rest of the Delta. In fact, conductivities here are often similar to the saline areas of the western Delta. In consequence the algal community is frequently more similar in these two areas than in the rest of the Delta. The algal community from 1969 to 1974 was dominated by *Thalassiosira*, *Cyclotella*, *Chlamydomonas* (= *Skeletonema*?), and *Melosira*. The 1984 community was similar, but at that time *Chlamydomonas* was abundant while *Skeletonema* was not reported.

Zooplankton of the Delta are moved around with the water so the animals from one river are often be found in the channels of another, leading to little distinctiveness in the plankton communities in any one area. The dominant zooplankton include the freshwater rotifers,

particularly *Keratella*, the cladocerans *Bosmina* and *Daphnia*, and the copepod *Cyclops*. The introduced *Sinocalanus* also occurs in abundance.

4.4 Organic carbon sources (see Appendix A for details)

4.4.1 South Bay

For the channel of South Bay during the period 1980-1987 there was no apparent trend in annual production. (Cloern 1990; Figure A.4 in Appendix A). Peak productivity varied markedly from one year to the next, but fluctuations in annual production were small.

Major decreases in tidal marsh did take place between 1850 and 1958 (Atwater et al. 1979), and tidal plants could have been a major organic carbon source in the nineteenth and early twentieth century. However, comparison of maps for 1958 and 1985 show a decrease of only about 1% in mudflat area and 10% in tidal marsh area during that period. Therefore, there is no evidence to suggest recent significant decreases in either benthic microalgal productivity or tidal marsh export of organic carbon.

Point source discharge is the only source with a detailed record for the years prior to 1980. The decrease has been quite remarkable (Appendix A, Fig. A.5), particularly since 1972 when the Federal Clean Water Act required a minimum of secondary treatment for all dischargers. The peak in organic carbon from this source in 1965 was almost exactly 10 times that in 1985. In view of the interannual variability in phytoplankton productivity, municipal wastewater could have been one of the dominant organic carbon sources for the South Bay during the 1960s and early 1970s, at least for years when microalgal activity was low. It is clear that point source discharge no longer plays a large role in the organic carbon supply for South Bay.

Regions in South Bay which receive higher sewage loads per unit area may show greater importance of point source discharges of carbon, either now or in the past. However, separate estimates for phytoplankton productivity and other processes in these zones are not available for comparison.

Assuming that the South Bay food web is now driven primarily by energy from phytoplankton and, perhaps, benthic microalgae, the controls on year-to-year fluctuations in primary productivity are of great interest. Nutrient concentrations typically exceed levels that limit phytoplankton growth rates and are thus not a factor (Conomos et al. 1979). In the absence of nutrient limitation, productivity can be shown to depend on three variables: surface irradiance, the proportion of the water column in the photic zone, and phytoplankton biomass. This is also true of many other estuaries (Cole and Cloern 1984; Cloern 1987; Cole and Cloern 1987).

Cloern (1979, 1982, 1984) and Cloern et al. (1985) hypothesized a mechanism contributing to interannual variability in South Bay based on the depth of the photic zone and

phytoplankton biomass. When periods of high Delta discharge in winter-spring coincide with periods of low tidal current speed during the tidal cycle, South Bay waters stratify. The mixed layer becomes smaller, and more of the phytoplankton are held higher in the water column. In addition, heavier suspended particles sink out of the stable surface layer and turbidity decreases, resulting in a deeper photic depth. The result is an increase in the growth rate in the mixed layer. Phytoplankton in the mixed layer also become effectively isolated from benthic molluscs, polychaetes, and other suspension feeders, which otherwise are capable of filtering the entire water column daily. Phytoplankton biomass is thus allowed to rapidly increase.

If this mechanism is an important source of interannual variability, there should be a relationship between annual phytoplankton productivity in South Bay and Delta discharge. Cloern (1990) provided evidence for this relationship using estimates of net photic zone productivity in the channel for the period 1980-1987. The linear relationship between discharge and productivity accounted for 65% of the variability. The statistical evidence supports the hypothesis that river discharge contributes to interannual variability of phytoplankton productivity in South Bay. It should be noted, however, that the effects of river outflow are heavily damped and that variability in annual production in South Bay channels varies only by a factor of two.

However, about half of South Bay may be too shallow for this stratification mechanism to operate, and over 60% of the annual phytoplankton production takes place in these shoal areas. In addition to Delta-derived intrusions of turbid water, local streams, runoff and resuspension of sediments (Conomos et al. 1979) may play a role in reducing productivity in shallower waters on a seasonal basis. Resuspension of chlorophyll (Thompson et al. 1981) also may contribute to variability in algal biomass.

The recent appearance of the Asian corbulid clam *Potamocorbula amurensis* (Carlton et al. 1990) introduces a new element of uncertainty, particularly for South Bay south of the Dumbarton Bridge. *Potamocorbula* is currently present, but not abundant, in South Bay both north and south of the bridge (Carlton et al. 1990). According to a synoptic survey in 1973 (Nichols 1979; Thompson and Nichols 1981), benthic invertebrate biomass south of the bridge was 50% less than biomass north of the bridge in summer, 80% less in winter. Organic carbon sources have not yet been tallied for the lower South Bay independently. Little reason exists, however, for expecting a lower food supply, particularly as tidal marsh export, point source discharge, and runoff are probably much higher here than for South Bay as a whole. A potential may be present for higher benthic biomass, increased grazing pressure, lower phytoplankton biomass, and reduced phytoplankton productivity. *Potamocorbula* perhaps can exploit this opportunity because of its apparent ability to withstand a much wider range of sediment types and salinity than other benthic macroinvertebrates (Carlton 1990). In South Bay north of the Dumbarton Bridge, on the other hand, benthic biomass is more typical of intertidal communities (e.g. Knox 1986b). *Potamocorbula* may very well displace certain members of the current estuarine invertebrate community, but the total biomass and consequent grazing pressure may not change

dramatically. Note that interannual variability is high among the benthos, despite the absence of long-term trends (Nichols and Thompson 1985b); thus, the applicability of the 1973 data to subsequent years is actually unknown and the suggestions made here highly speculative.

4.4.2 Central Bay

No long-term chlorophyll series exist to adequately characterize interannual variability of either phytoplankton or benthic microalgae in Central Bay. Although wastewater discharges must have been a significant source of organic carbon in the recent past, point source discharges no longer appear to play an important role in the carbon budget of Central Bay. Based on the movements of materials through Central Bay from adjoining subembayments and the coastal ocean, Central Bay can be expected to show different patterns than each of the neighboring areas. The different natures and causes of interannual variability in each embayment make the patterns in Central Bay particularly difficult to predict or analyze.

4.4.3 San Pablo Bay

As in Central Bay, interannual variability of phytoplankton activity is difficult to characterize and to understand because of the paucity of long-term chlorophyll or productivity measurements in San Pablo Bay. During 1971-1973, chlorophyll samples were collected from both shoal and channel sites, but routine sampling has since been confined to channel sites. It is particularly unfortunate that no long-term data series are available for the shoals, as most annual phytoplankton production probably takes place in the shallower region. Based on the study of seasonality during 1980 (Cloern et al. 1985) and the chlorophyll data that do exist for San Pablo Bay (Ball 1987), interannual variability of phytoplankton has been attributed to processes similar to those of Suisun Bay. Point source discharges have never been important, even at their peak in 1970 (see Appendix A).

4.4.4 Suisun Bay

Transport of chlorophyll into Suisun Bay is strongly related to flow and this transport of riverine carbon may account for most of the available material at the base of the food web in Suisun Bay. Year-to-year fluctuations in riverine loading largely reflect the corresponding variability in Delta outflow. The drought period that began in 1987, in particular, is probably a time of highly reduced chlorophyll loading from Delta outflow.

Part of the organic material carried into Suisun Bay can be attributed to upstream point source discharges. Through the 1970s, the amount of this material declined by more than 75% (Hansen 1982). The significance of the decrease during the 1970s is uncertain. Recent measurements of biochemical oxygen demand in the water at Chipp's Island show no change through the same period; this suggests that upstream changes in municipal wastewater discharge did not affect the concentrations of organic material in Suisun Bay. The evidence is not conclusive, however, as the Chipp's Island station is subject to influences from within Suisun Bay as well as from Delta discharge.

Comparing primary productivity measures in 1988, a "very dry" year, with the data of 1980, an "intermediate" year, shows that productivity during 1988 was much lower than in 1980. Photic zone productivity fell by a factor of five at shoal and channel stations. This decreased productivity was due to lower phytoplankton biomass, not lower growth rates.

Phytoplankton productivity in Suisun Bay—even more so than for the other embayments—is overwhelmingly dominated by shoal productivity. Interannual variability in productivity must therefore reflect fluctuations in shoal, not channel, productivity. The decrease in productivity between 1980 and 1988 was largely attributable to biomass changes and not to a change in photic depth (which actually increased in 1988). If biomass is generally the controlling factor for productivity in Suisun Bay, it follows that shoal biomass fluctuations should be a guide to variability in embayment productivity. Long-term data for chlorophyll *a* at shoal stations in Grizzly Bay and Honker Bay suggest that phytoplankton productivity in Suisun Bay has been depressed since 1982-1983. Productivity in 1977 also appeared to be low.

As in San Pablo Bay, recent trends for tidal marsh area cannot be evaluated. Point sources, when they were four times higher in 1970 (Fig. A.5), may sometimes have been as significant as phytoplankton or tidal marsh sources, but even then they would have been secondary to loading from Delta discharge.

4.4.5 Sources of variability in productivity in San Pablo and Suisun bays

Contributions of organic material from Delta discharge depends on the volume of discharge and on the riverine concentrations of organic materials. Despite large-scale changes in the abundance and composition of riverine phytoplankton (see Ball 1987 for a detailed analysis), annual chlorophyll concentrations in recent years appear to be largely proportional to annual Delta discharge. Variability in river-borne phytoplankton is evidently inadequate to mask the effects of flow volume.

Phytoplankton productivity in Suisun and San Pablo bays is controlled by shoal phytoplankton biomass. Two processes control interannual variability. The first is the effect of Delta outflow on the residence time for phytoplankton biomass. Much of the work on phytoplankton activity within the northern reach of San Francisco Bay has focussed on the significance of the entrapment zone resulting from estuarine circulation (Peterson et al. 1975). Net water column productivity is almost always negative in the channel because of the small portion of the water column in the photic zone, so biomass must be imported for accumulation to take place. During periods of high Delta outflow, an entrapment zone forms in the channel of San Pablo Bay which increases the residence time of algae dispersed from shoals by tidal mixing and allows such biomass accumulation. As flows decrease, the entrapment zone moves into Suisun Bay where it performs a similar function. During particularly low flows, the entrapment zone is located in the western Delta. Arthur (1975) first hypothesized that positioning of the entrapment zone relative to large expanses of shoal area was the most critical factor regulating accumulation of phytoplankton in the zone.

Further work has largely borne out this contention (Arthur and Ball 1979, 1980; Ball 1977; Cloern et al. 1983, 1985; Catts et al. 1985; Ball 1987).

The spatial distribution of primary productivity need not reflect that of biomass. When an entrapment zone is present, the residence time for certain phytoplankton and detrital particles is increased and physical transport losses are smaller. Perhaps even more important, the concentration of food particles permits more efficient feeding by planktivores in the zone. Nonetheless, in the deeper river channels, the zone may still be an area of reduced or even negative primary productivity because a high proportion of the water is out of the photic zone. For the entrapment zone to stimulate primary productivity, shoal residence time must be increased: by decreasing the gradient of biomass between shoal and channel, the entrapment zone probably suppresses net mixing losses of biomass from the shoals. The close relationship between shoal and channel chlorophyll testifies to the thorough mixing between the two regions.

The relationship between the entrapment zone and shoal biomass (and, presumably, productivity) is not a simple one. Rather than determining a unique biomass, the location of the entrapment zone appears to set bounds on a range of possible biomass levels. River flow therefore controls the range of possible chlorophyll concentrations, and this range is more restricted both at high flows and at low flows. The maximum chlorophyll concentration occurs at about $250 \text{ m}^3 \text{ s}^{-1}$, the approximate center of the flow range that positions the entrapment zone in Suisun Bay. But chlorophyll values are quite variable within the range and it is clear that positioning of the entrapment zone is not the whole story.

An additional source of interannual variability in biomass appears to be consumption by benthic herbivores. Nichols (1985) detailed how the Atlantic soft-shell clam *Mya arenaria* and other estuarine benthic invertebrates become established in Suisun Bay during drought periods such as 1976-1977. The larvae are carried upstream in the river-induced gravitational circulation and are able to colonize sites in Suisun Bay when salinity increases during dry years. In 1977, the estuarine species achieved densities sufficient to filter the entire water column approximately once per day. Similar appearances of *Mya* in 1962, 1979, and 1985 in Grizzly Bay suggest that about 16 months of consecutive low river inflow were necessary for successful colonization to take place (Nichols et al. 1990). The return of higher inflows eliminates estuarine species, resulting in decreased feeding pressure from the benthic invertebrate community.

This relationship between prolonged low river flow and temporary invasion by estuarine benthic invertebrates may have been upset in 1987 by the appearance of the Asian corbula clam *Potamocorbula amurensis* (Carlton et al. 1990). The clam was probably introduced from the western Pacific by the release of seawater ballast into San Francisco Bay in the mid-1980s. By 1987, *Potamocorbula* had become numerically dominant at shoal and channel sites in both Suisun and San Pablo bays, and was also present at some South Bay sites. The rapid spread has been attributed to a depauperate benthic community following the flood of early 1986, which resulted in a lack of competition from pre-existing species (Nichols et

1990). Low river inflow had again become prolonged for a period of 16 months by 1988, but *Mya arenaria* did not appear in its usual numbers, apparently excluded by the new arrival.

Low phytoplankton productivity may persist as long as conditions—namely low freshwater flows—favor estuarine benthic macroinvertebrates. Although riverine loading probably will increase once flows are restored, the same cannot be said of phytoplankton productivity. *Potamocorbula amurensis* is able to tolerate an extremely wide range of salinity (at least 1-30 ‰ [this symbol represents 'parts per thousand' also equal to mg salt per liter of water]), suggesting that it will not be dislodged by the return of higher river inflows (Nichols et al. 1990). If so, enhanced grazing pressure from benthic invertebrates will continue, depressing local populations of phytoplankton and perhaps benthic microalgae. Lower microalgal productivity could therefore persist for some time.

As long as Delta discharge is low, organic carbon contributions from riverine sources should remain at depressed levels as well. As a result, the relative importance of organic carbon from riverine loading can only increase. Given the apparent dependence of chlorophyll on annual Delta discharge, the relation between organic carbon sources for the food web and the magnitude of Delta discharge may thus become even more clear with the presence of *Potamocorbula*.

The response of marsh export to river discharge is of interest. The magnitude of Delta outflow undoubtedly has some moderating effect on exchange between tidal marsh and open water. The smaller freshwater supply during drought conditions also should favor the spread of estuarine macrophytes in their competition with freshwater macrophytes, changing the habitat areas available for higher organisms. But if the net effects on marsh export are damped compared to the response of organic matter loading and phytoplankton productivity, then marsh export may increase in importance during drought periods.

4.4.6 Delta

Phytoplankton is the dominant source of primary productivity in the Delta. The steep-sided banks of the dredged sloughs and channels have greatly reduced the former contributions of emergent vegetation and their attached assemblages of algae. Benthic algae are very limited in the Delta because of the combination of turbid water and depths that usually keep the euphotic zone well above the bottom. Dikes and dredges have removed most of the shallow habitat necessary for benthic algae or emergent vegetation from most of the Delta.

Substantial *in situ* production of phytoplankton occurs in the Delta. As it enters the Delta, water from the Sacramento River seldom contains phytoplankton concentrations greater than 6 $\mu\text{g/L}$, halfway through the Delta chlorophyll-*a* concentrations average 10-12 $\mu\text{g/L}$, and as it enters Suisun Bay it may carry from 10 to 60 $\mu\text{g/L}$ (Ball 1975;

Chadwick 1972). This pattern of increasing phytoplankton abundance at greater distance downstream occurs throughout the length of the Sacramento River (Greenberg 1964).

Conversely, at times when San Joaquin River water carries phytoplankton concentrations of 240 $\mu\text{g/L}$ into the Delta at Vernalis, phytoplankton populations in more downstream sites are only 40 to 60 $\mu\text{g/L}$. These results are primarily a result of the CVP and SWP pumping stations that withdraw almost all the plankton-rich waters of the San Joaquin (Ball 1975), thereby causing the less fertile waters of the Sacramento to flow up the lower channels of the San Joaquin.

As with Suisun Bay it is possible to document the decline in contribution of organic materials from improved sewage water treatment but there are insufficient data to allow estimation of the importance of such inputs to the food web of the Delta.

4.5 Trends in Zooplankton

Zooplankton populations are only sampled regularly in Suisun Bay and the Delta. The only data describing zooplankton populations in the rest of the Bay complex are for only one year each in South, Central, and San Pablo bays, so no statements of trends are possible. Trends in data on zooplankton in the upper estuary have been analyzed as part of testimony for the State Water Resources Control Board (CDF&G 1987b) for the period from 1972 to 1985. A more recent analysis of data up to the introduction of the clam *Potamocorbula* is being developed and generally agrees with the trends reported in 1987 (Orsi et al. 1991). The following discussion draws on both reports and on our own graphing of the data.

4.5.1 Rotifers

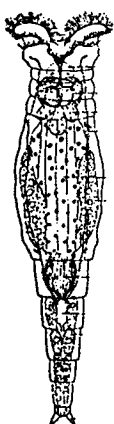


Figure 5
Ventral view
of typical
rotifer, length
about .1mm
(modified
from Pennak
1953)

The Rotifera are microscopic multicellular invertebrates (Figure 5) most common in fresh waters, although a few purely marine forms are known. The overwhelming majority of species are sessile and associated with littoral substrates, but about 100 species are planktonic and form a significant part of freshwater zooplankton communities. The anterior end is ciliated, and the movement of these cilia functions both in locomotion and in directing food particles toward the mouth. Omnivorous feeding on both living and dead particulate organic matter is typical, but some species prey on protozoa, other rotifers, and other zooplankton. Reproduction is typically by parthenogenetic females, occasionally punctuated in some species by sexual reproduction involving short-lived males. Dominants in the Bay-Delta include the common genera *Synchaeta*, *Keratella*, and *Brachionus*.

At salinities greater than 5-10 ‰, *Synchaeta* is the most common rotifer, so it is common in South Bay with its distribution in the rest of the Bay varying seasonally (Ambler et al. 1985). It is usually found in abundance only in areas with high densities of chlorophyll *a* (Ambler et al. 1985). In the upstream portions of the estuary, rotifer populations undergo seasonal cycles that appear to be a result of seasonal changes in salinity (Chadwick 1972). Thus, *Keratella* is abundant in the western Delta only in the spring when salinities are minimal (Chadwick 1972), and in the fall *Synchaeta* dominates (Siegfreid et al 1978). In the eastern Delta, beyond usual salinity intrusion limits, a rich rotifer assemblage occurs, *Keratella* being most abundant in an array of eight genera of herbivores, omnivores, and one predatory genus, *Asplanchna* (Orsi and Mecum 1986; Herbold and Moyle 1989). However, many of the additional rotifer species comprising the richer assemblage of the Delta are benthic rather than planktonic (Chadwick 1972).

Rotifer populations have sharply declined throughout the Delta, particularly in the San Joaquin River where they were formerly most abundant (CDF&G 1987d; Orsi et al 1991).

From 1972 to 1979 the population in the Delta declined to less than a tenth of their initial densities (Figure 6). In Suisun Bay, where they were never very abundant, the decline was less severe. Since 1979 there has been no consistent difference in abundance of rotifers in the two areas. This decline has been less in the more marine species *Synchaeta bicornis*, than in the more freshwater genera *Keratella*, *Asplancha*, and *Polyarthra* (Orsi et al. 1991).

The decline in the Delta appears to be strongly associated with declining concentrations of chlorophyll *a*, which formerly characterized the areas of greatest rotifer abundance (CDF&G 1987b).

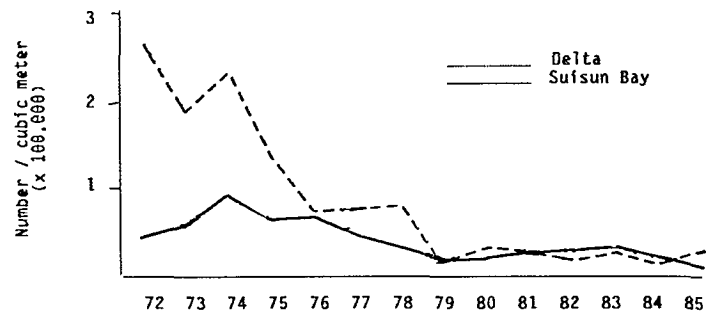


Figure 6 Mean densities from March to November of rotifers in 100,000 m⁻³ all species combined, in Suisun Bay (solid line) and the Delta (dashed Line). Modified from CDF&G 1987b.

The most abundant rotifer in both the Sacramento and San Joaquin rivers was *Keratella* in the early years of the study, it, along with the less abundant genera *Polyarthra* and *Trichocerca*, underwent massive declines in abundance through the 1970s (Figures 7, 8). *Synchaeta*, the rotifer most abundant in Suisun Bay and least abundant in the Delta, did not decline as precipitously. In Suisun Bay, densities of all of the more abundant types were present at much lower densities through the 1980s than in the 1970s (Figure 9). The less common species of the genus *Synchaeta* are the only group to show no trend through time, although they also fall to record low densities in 1988, coinciding with the establishment of *Potamocorbula amurensis* in high densities.

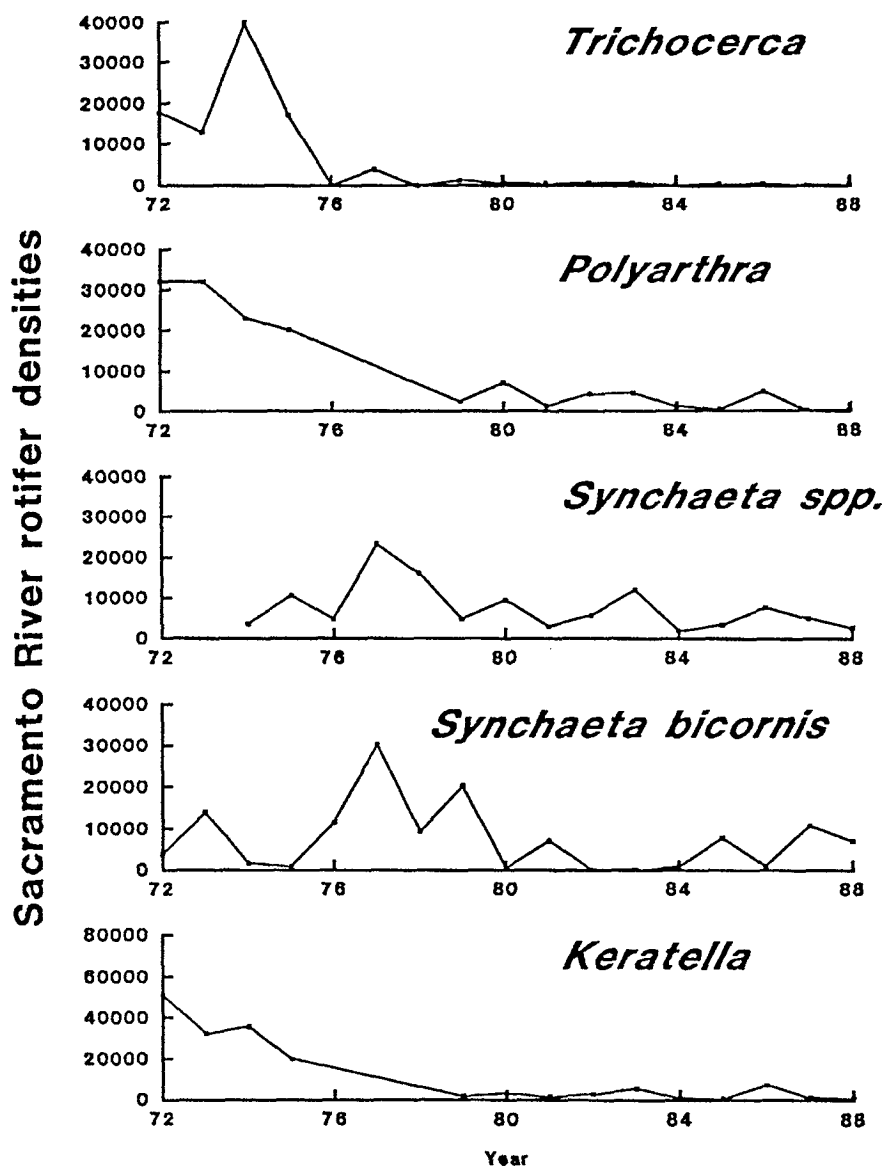


Figure 7 Mean densities per m³ of the abundant species of rotifers by year in the Sacramento River (data provided by CDF&G)

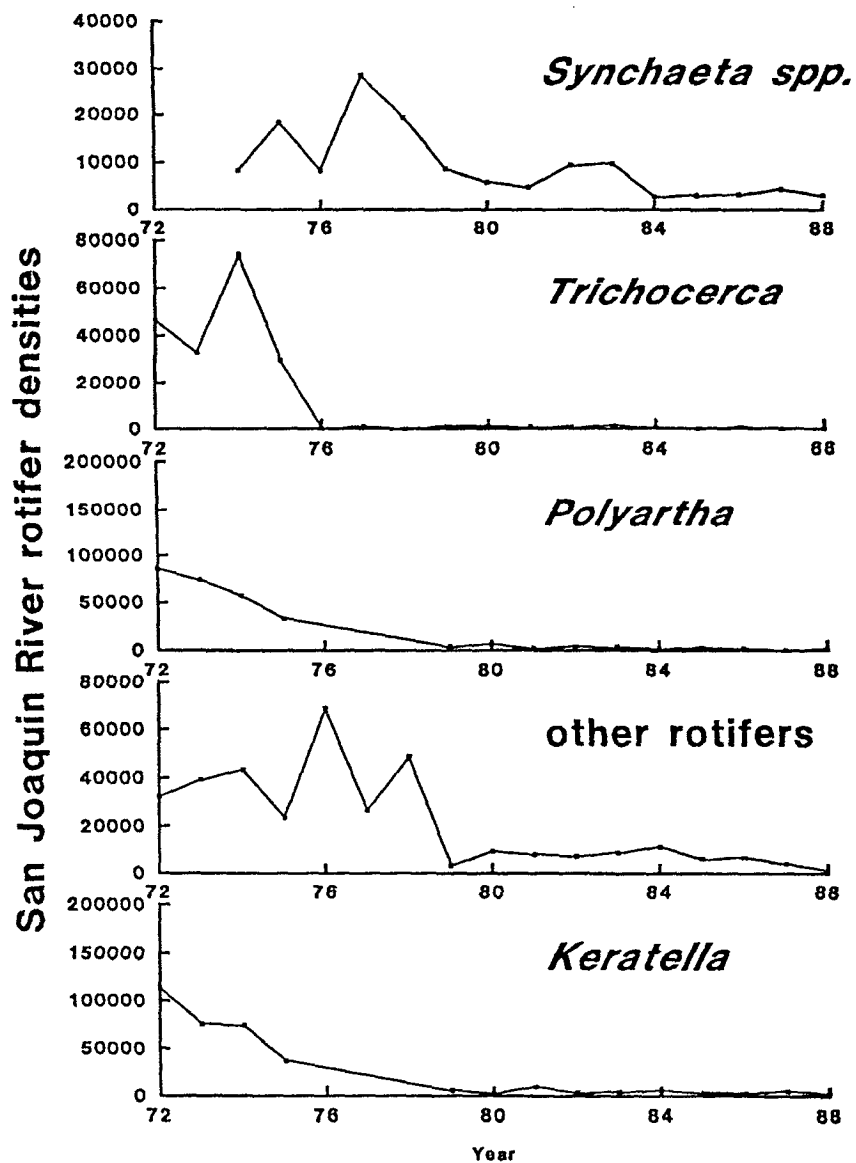


Figure 8 Mean densities per m³ of the abundant species of rotifers by year in the San Joaquin River (data provided by CDF&G)

Suisun Bay rotifer densities

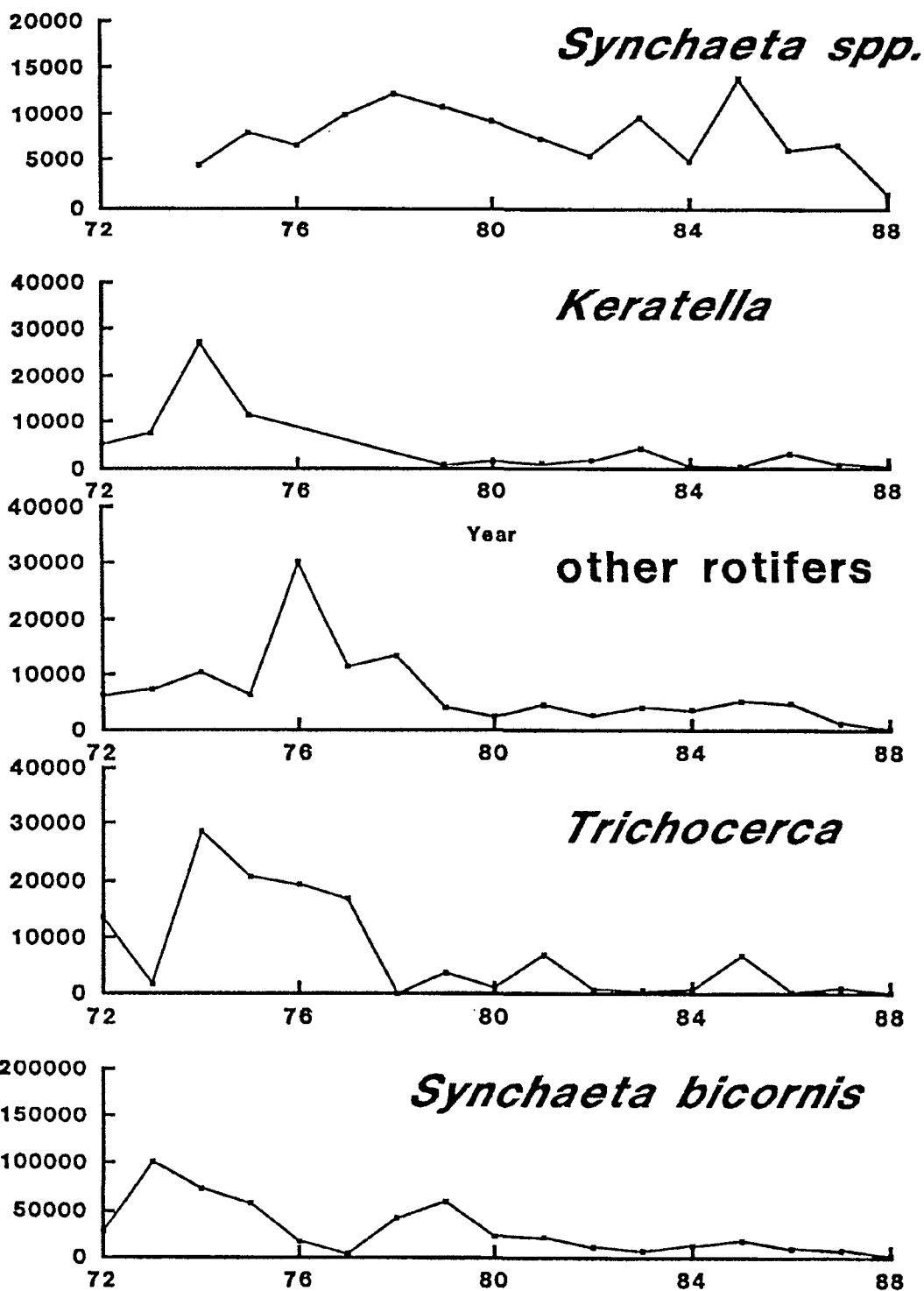


Figure 9 Mean densities per m³ of the abundant species of rotifers by year in Suisun Bay (data provided by CDF&G).

4.5.2 Crustaceans

Crustacean zooplankton have been the subject of much more study in Suisun Bay than any other area because of the importance of opossum shrimp (*N. mercedis*) as a principal food of young striped bass (Turner 1966a; Siegfried and Kopache 1980; Knutson and Orsi 1983; Orsi and Mecum 1986; Orsi et al. 1991). Studies describing copepod species and documenting their distribution have also contributed to general understanding of trophic dynamics in the Estuary (Orsi et al. 1983; Ferrari and Orsi 1984; Orsi and Mecum 1986). Laboratory studies arising from field observations have examined factors affecting the links between trophic levels (Meng and Orsi 1991).

Studies of plankton in the Delta and in the Lower Bay have been much more scarce. The only recent publication describing Delta zooplankton was that of Orsi and Mecum (1986) which ended with a recognition that invading species of copepods had drastically changed the zooplankton community from what they were describing. Evidence presented to the State Water Resources Control Board hearings (CDF&G 1987d) described long-term trends in Delta zooplankton through 1985. Very little has been published on riverine plankton, and what little has been done focussed more on phytoplankton (Greenberg 1964). Analyses of recent Delta zooplankton data are in preparation (Orsi et al. 1991). Zooplankton in Central, South, and San Pablo bays were described on the basis of the years 1978-1981 (Hutchinson 1981a, 1981b, 1982a, and 1982b; Ambler et al. 1985). Zooplankton distribution and population dynamics in coastal waters near San Francisco Bay have been studied as part of intensive studies of Dungeness crab biology (Hatfield 1983a; Reilly 1983).

4.5.2.1 Cladocera

Cladocera, or water fleas (Figure 10), are often the most abundant crustaceans in fresh water. Most species are widely distributed throughout large areas, including all of the species reported from the Sacramento-San Joaquin Estuary. Typically, cladoceran populations show strong seasonality in abundance and pronounced changes in reproductive habits in different seasons. During the warmer months of the years reproduction is by parthenogenesis and the females give birth to fully functional juveniles. Gestation times are around two days and generation times are usually less than one month. Thus, a population can rapidly increase under favorable conditions. Males and the larger eggs which they fertilize (called ephippia) are usually produced as temperatures

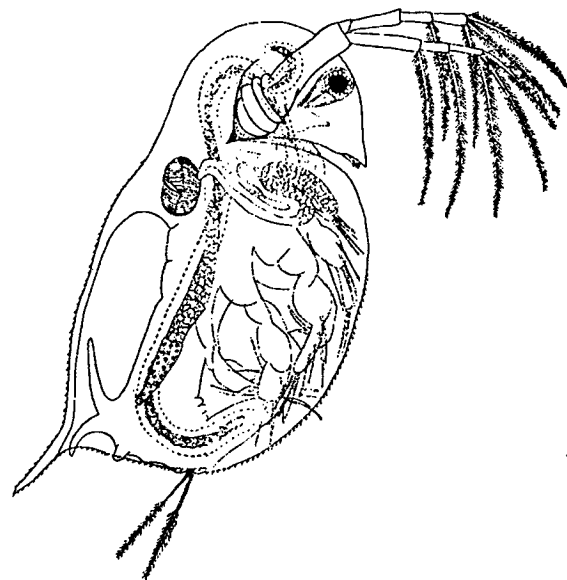


Figure 10 *Daphnia pulex*, usually 1-3 mm (modified from Pennack 1953)

and photoperiods decline. The fertilized ephippia sink to the bottom and are the primary method of overwintering for these animals. Ephippia are resistant to desiccation and, by massive attachment to waterfowl, are responsible for the wide distribution patterns of most Cladocera. Various morphological features of the ephippium appear to facilitate dispersal by fish or waterfowl (Dodson and Frey 1991). Once in a suitable habitat, the ephippium develops into a parthenogenetically reproducing female. Thus, successful colonization of a new habitat can be accomplished by transport of a single ephippium.

Cladocera swim by sudden contractions of their antennae and are efficient feeders on a wide variety of materials from throughout the water column, including phytoplankton, bacteria and colloidal suspensions. They are widely recognized as an important level for food chains in the upper portions of estuaries (Haertel and Osterberg 1967).

Cladocera seldom occur in abundance in areas where salinity is greater than 1 ‰ [electrical conductivities] $EC > 600 \mu S/cm$), and are therefore more abundant in waters of the Delta than in Suisun Bay. All cladocerans have the bulk of their populations at conductivities under $1000 \mu S/cm$ and there is no apparent separation of the genera by conductivity within the small range within which they all live (Figure 11). Of the three most commonly collected species of Cladocera, *Bosmina longirostris* is the most abundant species throughout the Delta, *Daphnia pulex* (with *D. schodleri* and *D. galeata*) is less abundant and none of its population is found within a narrower range of salinities, *Diaphanosoma euchenbergianum* is least abundant but a larger proportion of its population is found at higher conductivities (Figure 11). *Bosmina* is the most widely distributed genus, occurring at measurable densities in Suisun Bay in all but two of the years since sampling began in 1972 and in 6 of the 10 years of sampling in Carquinez Strait (unpublished data CDF&G). Abundance of *Bosmina* may be partly controlled by the abundance of the predaceous shrimp *Stomatopoda* (Orsi and Mecum 1986). *Daphnia* also has been found in Suisun Bay in all but two years of the sampling, but it occurs at extremely low densities (less than 10 per cubic meter in half of the years). *Daphnia* was found at Carquinez Strait in only 4 of the 10 years of sampling there, almost solely during periods of high Delta outflow. Densities of all three species are highly correlated with temperature and, excluding *Diaphanosoma*, with chlorophyll *a* concentration (Orsi and Mecum 1986). These associations with temperature conform to the greater abundance of all species in the San Joaquin River, because it is generally warmer than the Sacramento River and supports higher densities of phytoplankton (Orsi and Mecum 1986). *Diaphanosoma* has the most restricted distribution of the three abundant native cladocerans; it has never been collected in samples taken at Carquinez Strait, and when collected in Suisun Bay its mean density has never exceeded 45 per cubic meter.

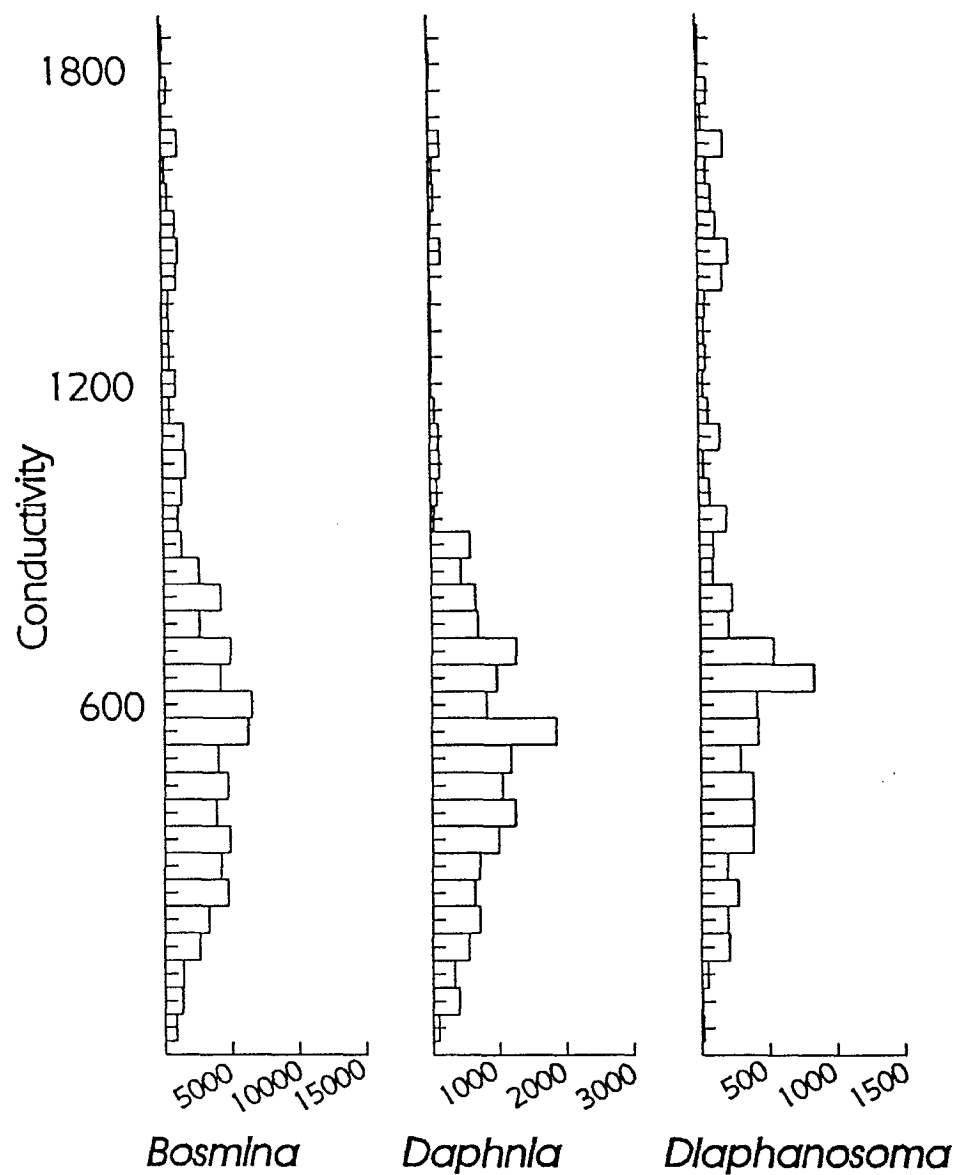


Figure 11 Mean catch (no. per cubic meter) of three species of Cladocera at different ranges of conductivities ($\mu\text{S/cm}$). (data from CDF&G).

Average densities of cladocerans have shown a long-term decline in abundance similar to that of the rotifers. The decline in cladocera is apparent in most genera except *Bosmina* and varies within different parts of the estuary. The decline in Cladocera appears to have been more sudden, occurring in the late 1970s as the rotifers in the Delta reached the end of their period of decline. Population densities have remained at rather constant low levels, but the lowest values for the three most abundant species all occurred in 1982-1983. A small recovery in abundance in all three taxa occurred through 1984-1986, but in recent years they have returned to extremely low levels.

Examination of the patterns of abundance of cladocerans through time for areas dominated by Sacramento River water, San Joaquin River water, and Suisun Bay shows the importance of outflow on cladoceran abundance and distribution. The sustained very high outflows of 1983 produced peak abundances of most cladoceran genera in Suisun Bay (Figure 1), although even these peaks are much smaller than the usual densities encountered upstream (Figures 13 and 14). The moderately high outflows of 1986 produced peaks in abundance for all genera within the Delta but had little effect on Suisun Bay populations. *Bosmina* is the most common genus of cladoceran and shows the smallest proportional change in abundance through time; the less abundant *Daphnia* and *Diaphanosoma* show much greater declines in abundance following 1977.

Suisun Bay cladocera densities

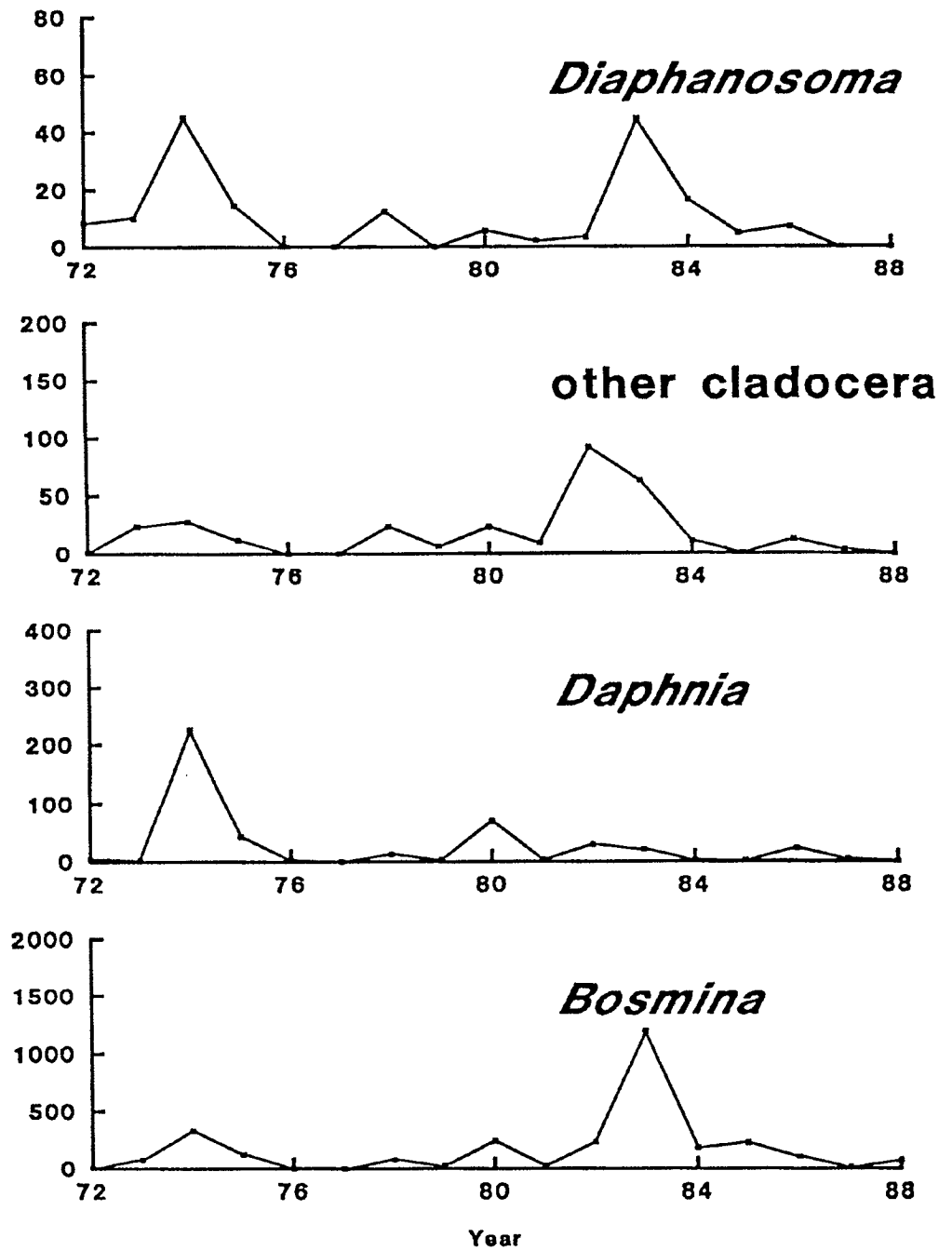


Figure 12 Mean densities of the three most abundant species of cladocerans in Suisun Bay (no./ per cubic meter). Data provided by CDF&G.

Sacramento River cladocera densities

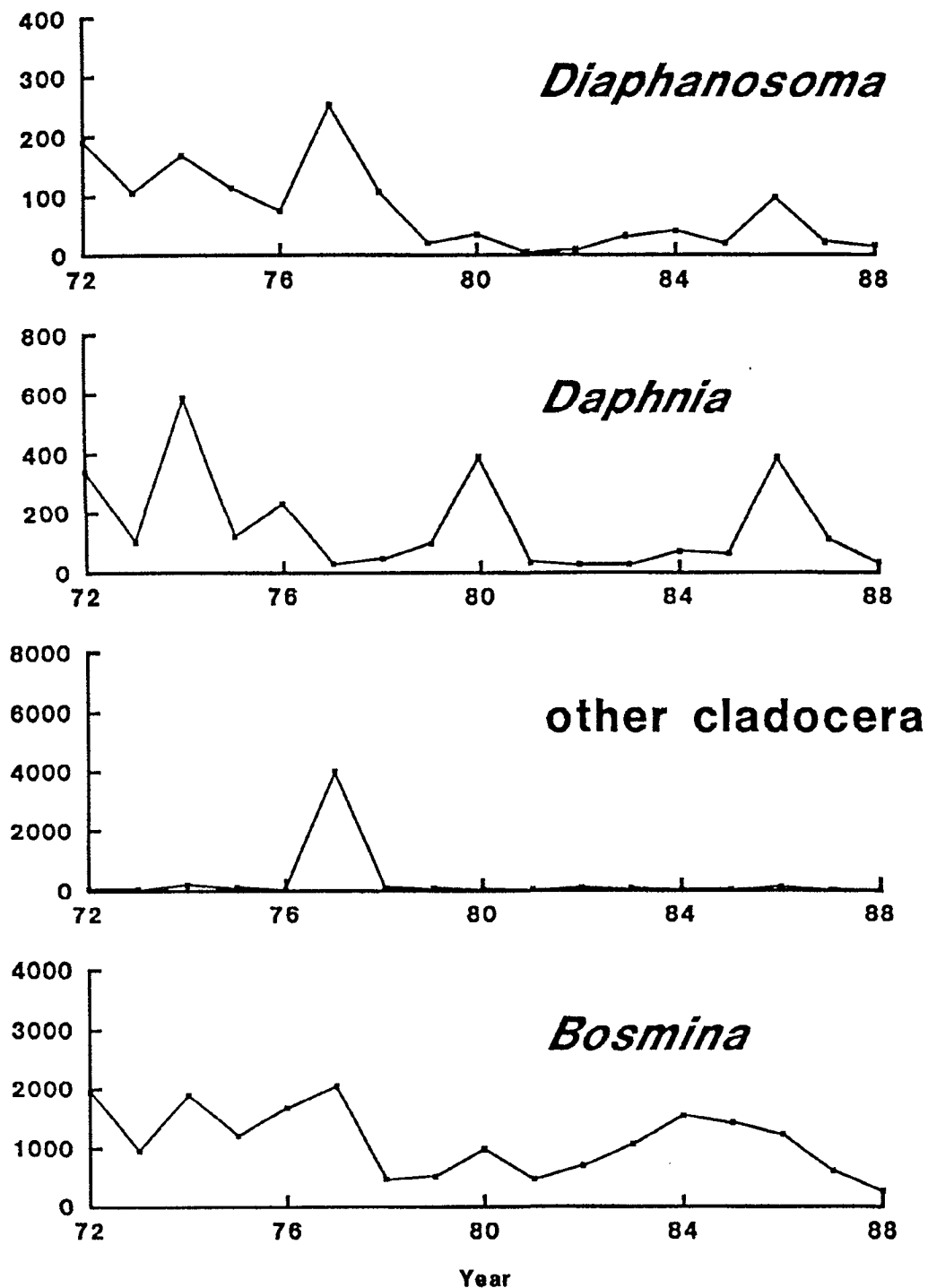


Figure 13 Mean densities of the three most abundant species of cladocerans in the Sacramento River (no./ per cubic meter). Data provided by CDF&G.

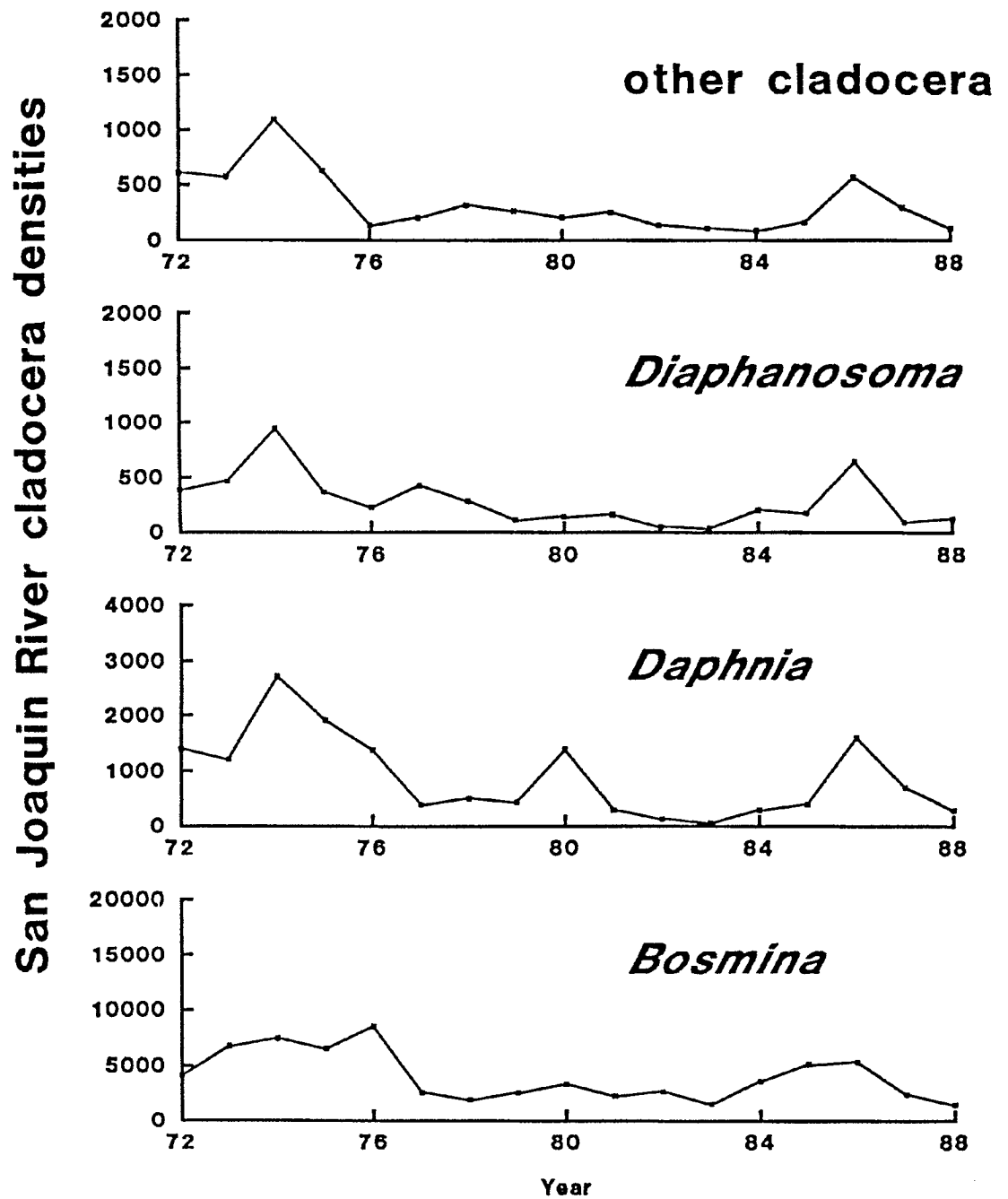


Figure 14 Mean densities of the three most abundant species of cladocerans in the San Joaquin River (no./ per cubic meter). Data provided by CDF&G.

4.5.2.2 Copepoda

Copepods are small crustaceans (Figure 15) that live in the water column like Cladocera but which are evolutionarily derived from oceanic animals so that their greatest diversity and abundance is in salt water. Harpacticoid copepods are predominantly benthic copepods and are not sampled very efficiently in studies of zooplankton. Calanoid copepods replace Cladocera in most of the Bay below Chipp's Island; cyclopoid copepods are generally found in more freshwater habitats with Cladocera. Calanoid copepods swim in a slow, smooth gliding pattern by movements of their mouthparts occasionally punctuated by sudden jerks propelled either by the same mouthparts or by their legs and antennae. Cyclopoid copepods move by a series of leaps propelled by flattened appendages on the abdomen and their first antennae, followed by a period of passively sinking (Williamson 1991). Cyclopoids respond to disturbance by escape responses that may involve hops at velocities up to 4 times that used in normal locomotion. Copepods are the primary food for many small fish in the Estuary, including larval striped bass.

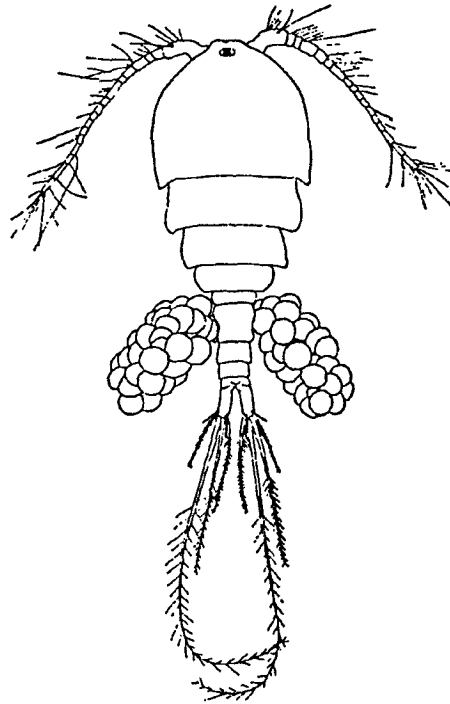


Figure 15 Typical cyclopoid copepod, 1-2 mm., with egg sacs. (Modified from Pennak 1953)

All copepods in the Estuary are sexual and cannot reproduce parthenogenetically, unlike rotifers and water fleas. However, females store sperm so a single mating can allow a female to produce a series of fertilized eggs (in the Calanoidea) or of eggsacs (in the Cyclopoidea). Development and incubation are generally rapid with sexual maturity attained in one or two weeks in most species and with hatching of eggs taking from 12 hours to 5 days. After hatching young copepods go through a series of molts as nauplii similar to some other crustacea and a further series of copepodid stages which resemble the adult. Rising temperatures and shortening photoperiods may prompt the production of thicker shelled, over-wintering eggs or larval stages may form cysts and fall to the bottom. Similarly, cyclopoids may also encyst at high water temperatures during the summer. Although most copepods are widely distributed, the lack of a specialized dispersal stage, like the cladoceran's ephippium, has apparently led to most freshwater and estuarine species being somewhat less widely distributed than most species of Cladocera. However, recent introductions of several species of copepods argues that larger cargo ships, with vast quantities of ballast water, have permitted widespread dispersal of coastal copepods. The abundance of exotic copepods in the estuary coincides with the change in trans-Pacific shipping to larger, canister carrying ships in the late 1970s.

In the Sacramento-San Joaquin estuary the abundant native copepods are sharply separated primarily by salinity (Figure 16) and season (Ambler et al. 1985). Figure 16 illustrates the distribution of catch from all collections averaged over the conductivities of the water where they were taken; abundance of a species at a particular station will depend on location, season, and amount of flow into the Bay. Note the much larger range of conductivities represented for copepods (in Figure 16) than for Cladocera (in Figure 11). The genus *Acartia* contains two species (*A. californicus* and *A. calussi*) which undergo complementary seasonal successions of abundance in South Bay (Ambler et al. 1985). Another species of the lower Bay (*Oithona davisae*) is not included in the figure but peaks in abundance in the autumn (Ferrari and Orsi 1984). In the late 1970s and 1980s populations of invading species, unintentionally introduced from China, *Sinocalanus doerri*, *Limnoithona sinensis*, and *Pseudodiaptomus forbesi* rapidly increased in abundance. Native copepods, particularly *Eurytemora affinis*, suffered large declines in abundance while these species have increased in abundance (Orsi et al. 1983; Orsi and Mecum 1986). In the Delta the dominant copepod genus was formerly *Cyclops* but is now *Pseudodiaptomus*.

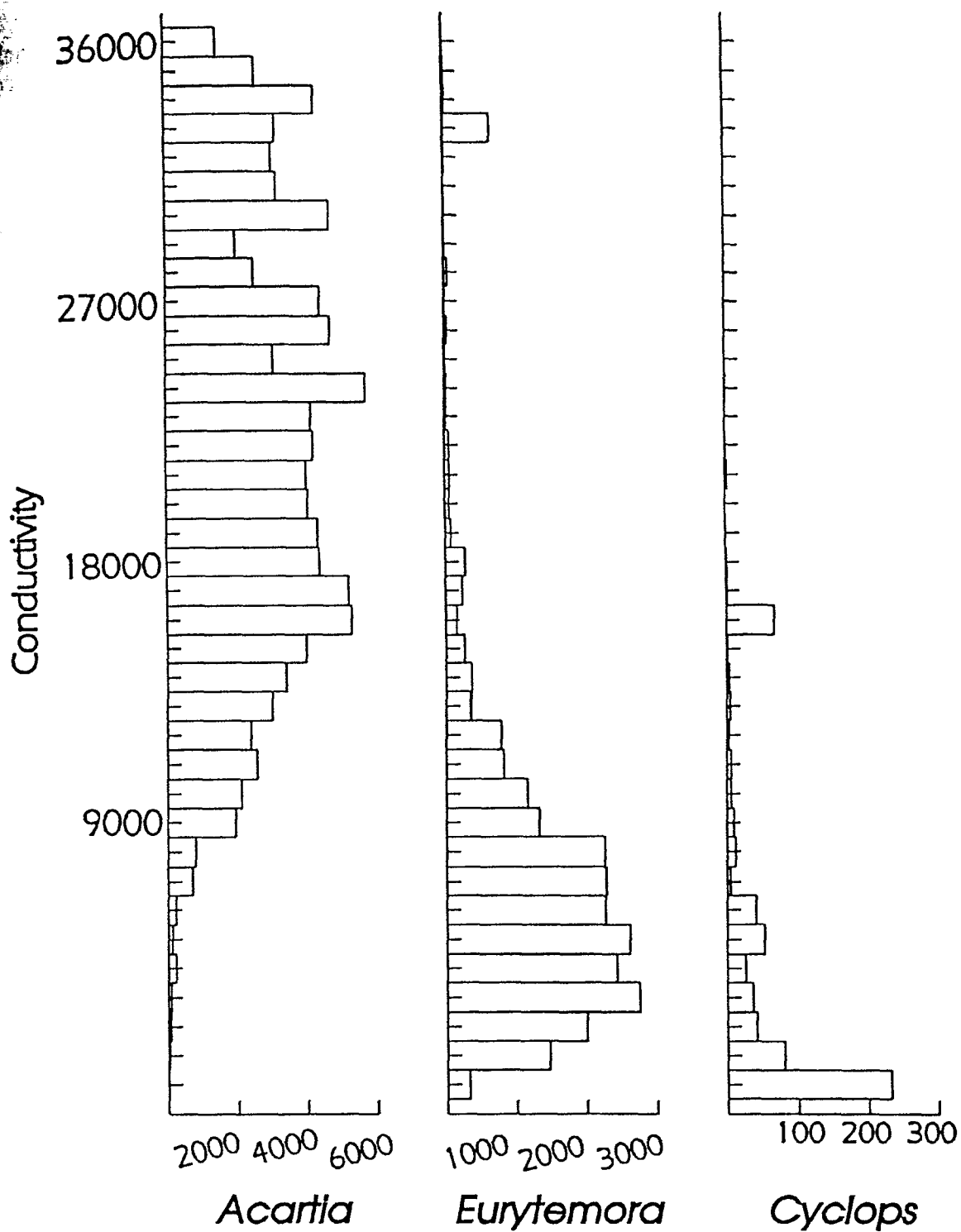


Figure 16 Mean catch ($\# \text{ m}^{-3}$) of three species of Copepoda at different ranges of conductivities ($\mu\text{S/cm}$). Data provided by CDF&G.

Most species of copepods have undergone severe, long-term declines in abundance (CDF&G 1987b). Only the marine species *Acartia* shows no evidence of a trend through time. This species is least abundant in the sampling area during years of high outflow and is usually most abundant when salinity in Suisun Bay is greatest (CDF&G 1987b). Invasion of the western Delta and Suisun Bay by *Sinocalanus doerri* in 1978 and by *Pseudodiaptomus forbesi* in 1987 was followed by declines in the abundance of *Eurytemora affinis* and the almost complete elimination of *Diaptomus* spp. (CDF&G 1987b; Meng and Orsi 1991). Most copepods, including *Acartia*, have been at record low abundances in Suisun Bay since the arrival and explosive spread of the clam *Potamocorbula amurensis*.

Analysis of the dominant native copepod species in waters of the Sacramento River, the San Joaquin River, and Suisun Bay shows that the decline is sharpest in the rivers (Figures 17, 18, and 19). *Eurytemora*, overall the most abundant copepod in both rivers, declined in abundance in 1978 and has remained generally below average densities of 500 l⁻¹ whereas in 4 of the 6 earlier years its average density exceeded 1000 l⁻¹. *Cyclops vernalis* and *Diaptomus* spp. show sharp declines through the 1970s in both rivers, although the *Diaptomus* decline stretches out to 1981 while *C. vernalis* was extremely rare by 1977. Both species showed a short-lived return to high density following the high outflows of February 1986. These mean densities are not adjusted for salinities, and simple changes in water quality due to low inflows may be adequate explanation for the declines.

The introduced copepods, *Limnoithona sinensis* and *Sinocalanus doerri*, are predominantly found in fresh water. Due to increases in the abundances of these species the average densities of copepods in each river are still high in most years (Figure 20). The simple replacement of native species by exotics is not a complete picture because *Sinocalanus doerri* inhabits stations further upstream than those occupied by the formerly abundant *Eurytemora affinis* (Orsi et al. 1983), so measures of average abundance are inflated by the greater range of the introduced species. Nonetheless, densities of native copepods are markedly lower in areas where introduced copepods are now abundant. Striped bass larvae prey more easily on native copepods than on introduced species, at least some of which have more effective escape responses (Meng and Orsi 1991). The introduced *Sinocalanus doerri* may be an additional predator on native copepods, as *S. tenellus*, a related species, has been shown to be an effective predator on nauplii (Hada and Uye 1991).

Within Suisun Bay only *E. affinis* shows a consistent pattern of decline through time, and the decline is not as severe as at upstream sites. The most abundant copepod in Suisun Bay, *Acartia*, showed increased abundance in dry years until recently. As in the rivers, *C. vernalis* fell to very low numbers in 1977 but was increasing to its former levels until 1987. All species in Suisun Bay were at extremely low abundances in 1988, when *Potamocorbula amurensis* was at high densities and chlorophyll *a* concentrations failed to attain their usual seasonal peaks. Introduced species of copepods are generally not a large part of the populations in Suisun Bay, but generally increase in abundance there in response to periods of high outflow (Orsi et al. 1983).

Suisun Bay (Figure 19) usually supports copepod densities about twice those found in the Delta (Figure 17 & 18). Average densities in Suisun Bay range from 2000-10,000 l⁻¹ while the average densities at river sites are usually between 1,000 and 4,000 l⁻¹. Although downstream transport of copepods is thought to be important in controlling the abundances of freshwater forms in downstream areas (Orsi et al. 1983; CDF&G 1987d) there is not an inverse relationship of copepod abundance in the different regions in wet years. The high flows of 1983 led to low abundances in all regions whereas the high flows of spring 1986 did not lead to any apparent shift of the populations downstream.

Sacramento River copepod densities

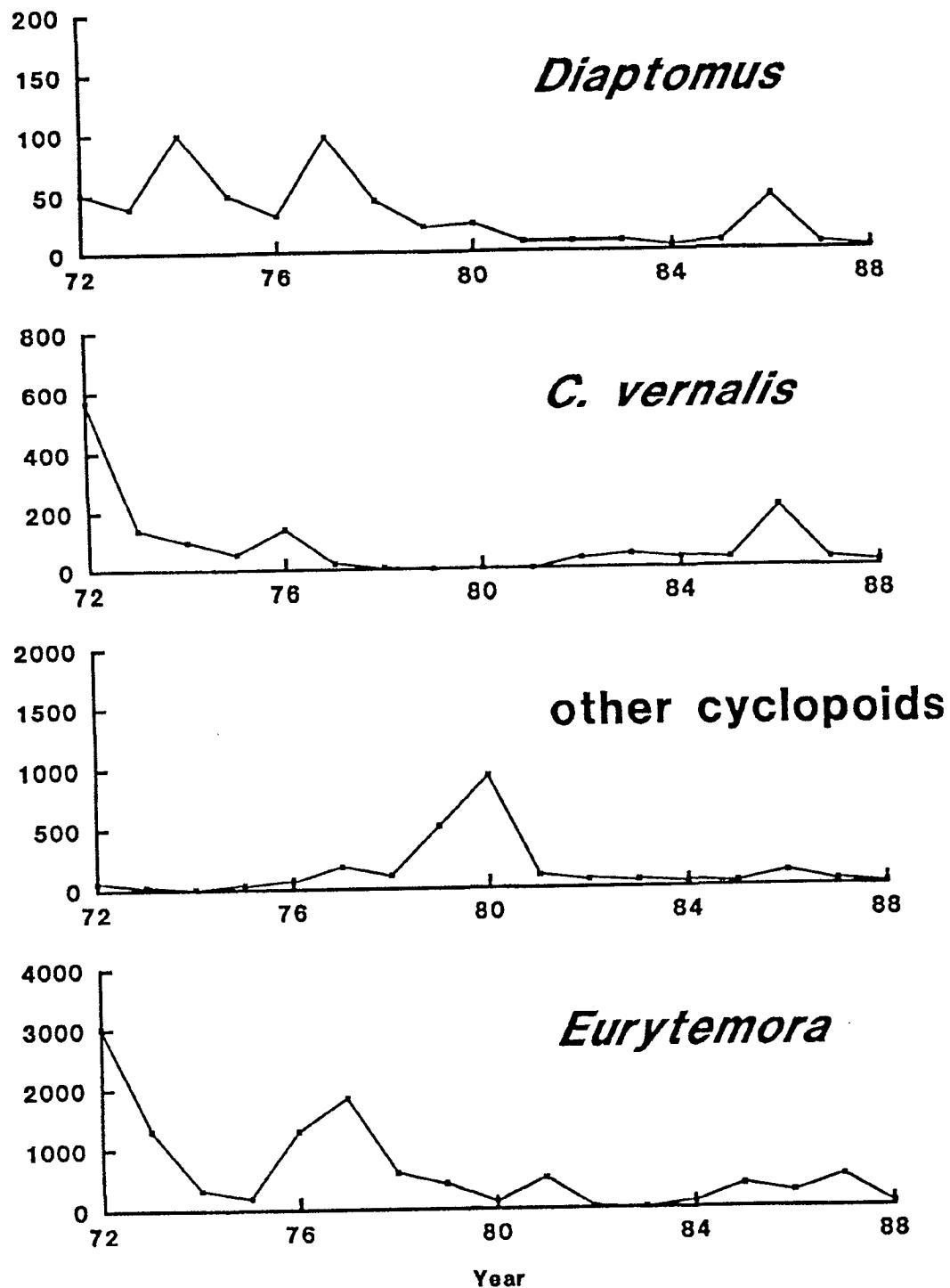


Figure 17 Mean densities of the four most abundant species of copepods in the Sacramento River (no./ per cubic meter). Data provided by CDF&G.

San Joaquin River copepod densities

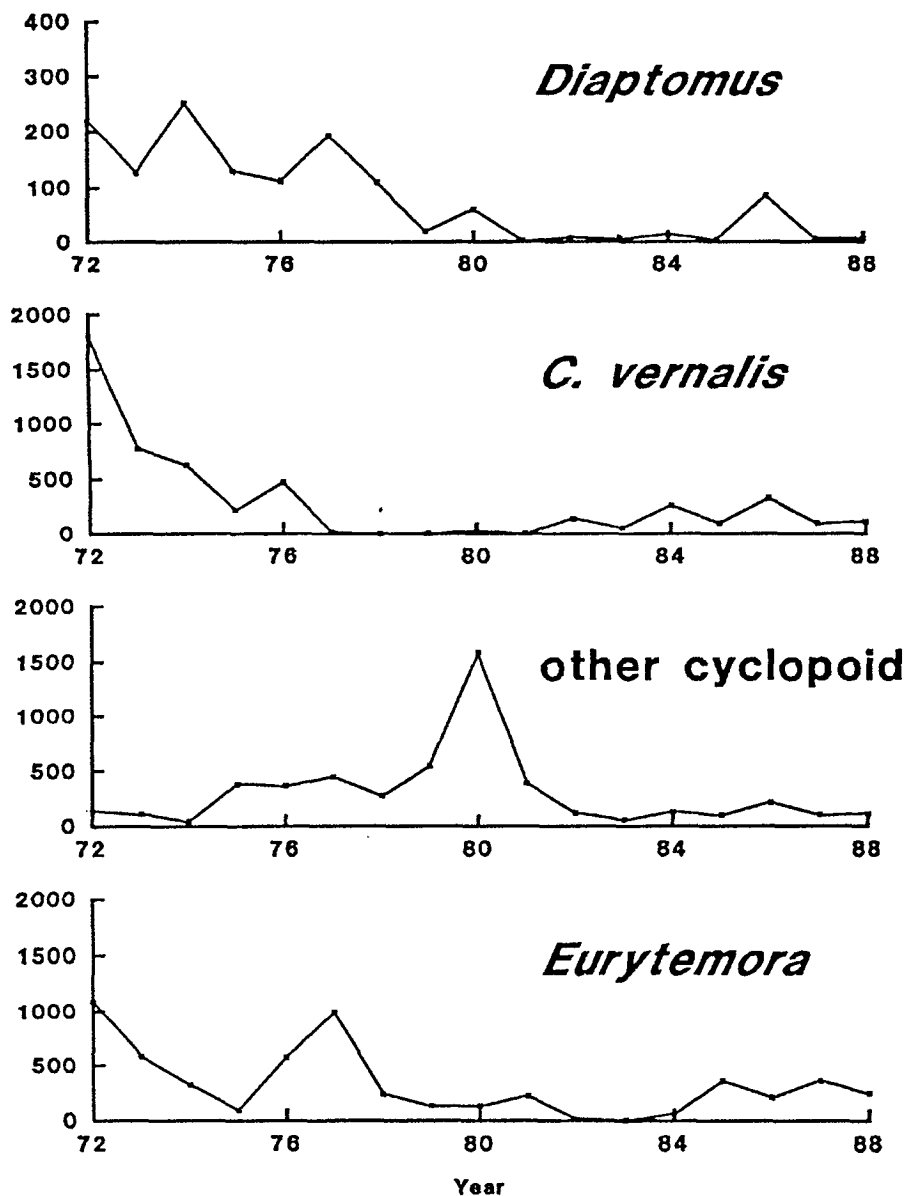


Figure 18 Mean densities of the four most abundant species of copepods in the San Joaquin River (no./ per cubic meter). Data provided by CDF&G.

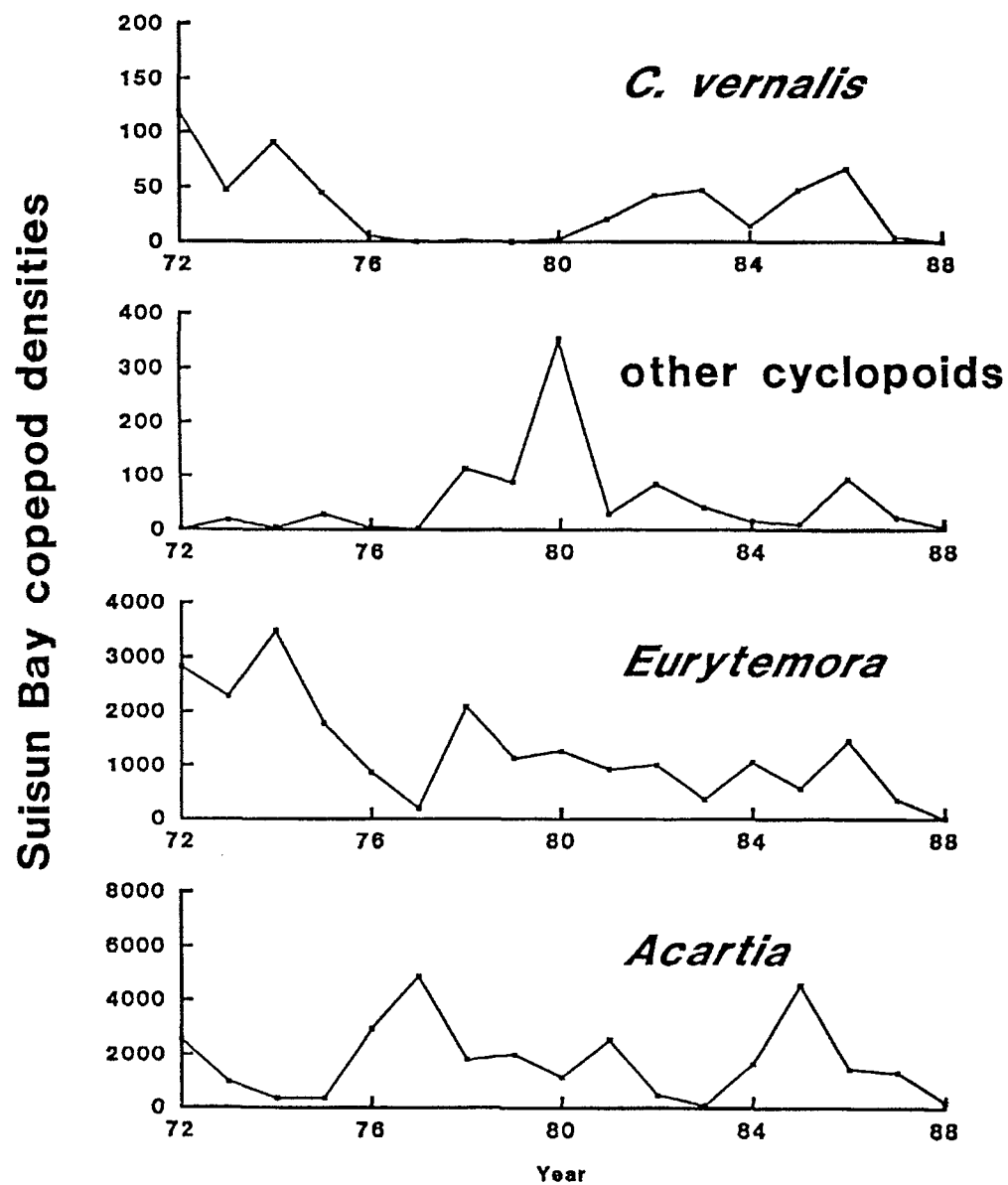


Figure 19 Mean densities of the four most abundant species of copepods in Suisun Bay (no./ per cubic meter). Data provided by CDF&G.

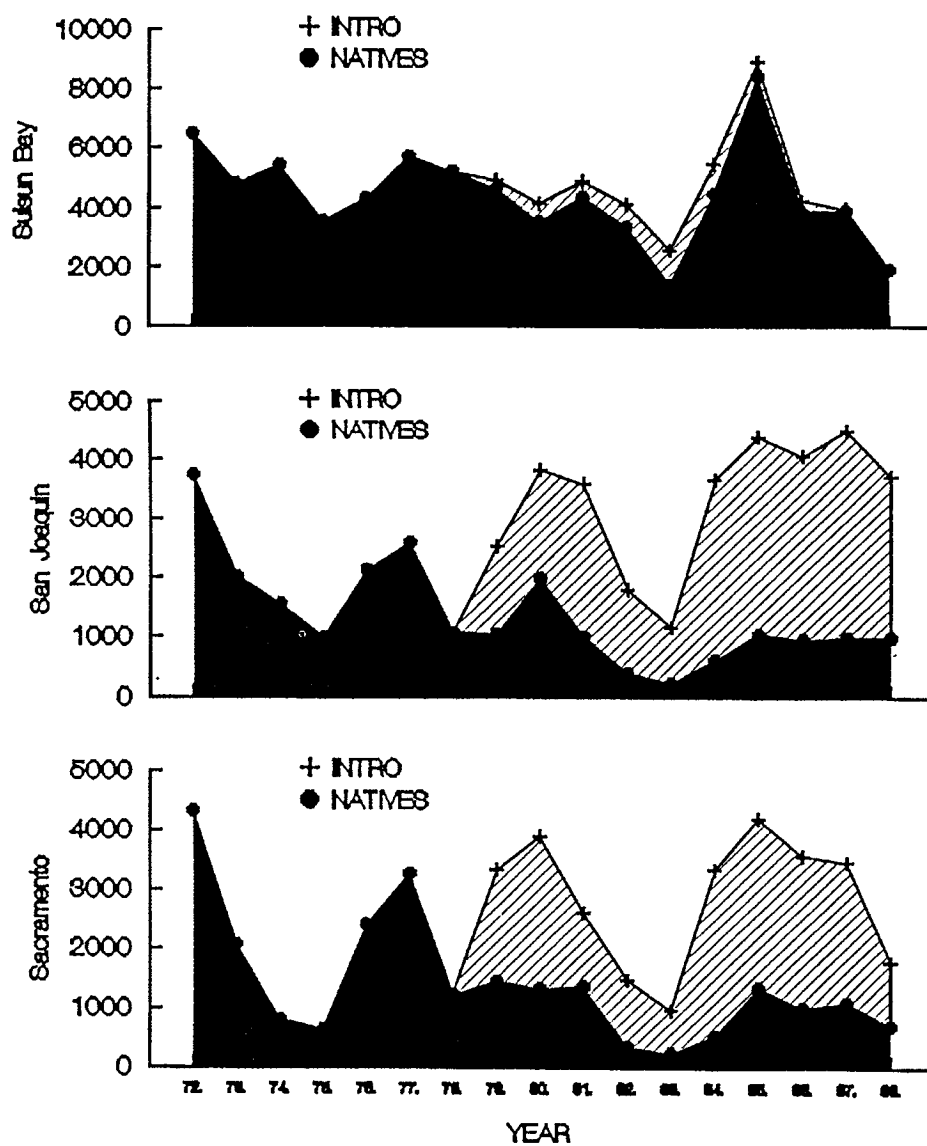


Figure 20 Comparison of densities (mean number per cubic meter) of native and introduced copepods in three areas: Sacramento River, San Joaquin River, and Suisun Bay (data provided by CDF&G)

4.5.2.3 Opossum shrimp

The opossum shrimp, *Neomysis mercedis* (Figure 21), is found in greatest abundance in Suisun Bay and the western Delta, although it is found as far upstream as Sacramento (Orsi and Knutson 1979) and in the lower reaches of the Mokelumne River (Heubach 1969). The family Mysidae is related to scuds and sowbugs, but is unusual in that its members are excellent swimmers and spend most of their lives in the water column. Mysid shrimp are found throughout the northern hemisphere and have been widely studied because they are important items in the diets of most fish where they occur and they have been found to be very useful in monitoring the effects of toxics.

Neomysis mercedis can be found from Alaska to just below Point Conception, California.

Opossum shrimp received their common name because females carry their eggs and young in a pouch at the base of the last two pairs of legs. Young are retained until the larvae are fairly well developed.

Neomysis mercedis is found in the diets of almost all fishes of the Delta (Heubach et al. 1963; Turner and Kelley 1966; Radtke 1966b; Turner 1966 a,b; Moyle 1976; Smith and Kato 1979; Stevens 1979; Moyle et al. 1985). In studies prior to 1974 these shrimp were identified by the synonymous names *N. atschwanensis* and *N. intermedia* (Simmons et al. 1974a,b). Unlike other elements of the zooplankton, the biology of *N. mercedis* has been widely studied and described. Another mysid shrimp is found in very low densities in the waters of San Pablo Bay, *Alienacanthomysis macropsis*. One small, very rare, and undescribed mysid has been found throughout Suisun Bay and the Delta (Orsi and Knutson 1979; Herrgesell pers. comm.), but there are no reports on the biology of either.

Early studies of the distribution of *N. mercedis* within the Delta found that it concentrated an inverse relationship of chloridity with abundance. During fall and winter mysids were most abundant at the most freshwater station, but from March to September densities were somewhat higher in areas with higher chloride concentrations (up to 2‰ but with a very sharp and significant decline at chloridities greater than 2‰). Greater abundance during summer in areas with chloridities just below 2‰ was particularly evident in the western Delta and, to a lesser extent, the San Joaquin River near Stockton (Turner and Heubach 1966; Heubach 1969). This observation was initially interpreted as evidence that salinity was a primary factor governing the distribution of the opossum shrimp. Later laboratory studies

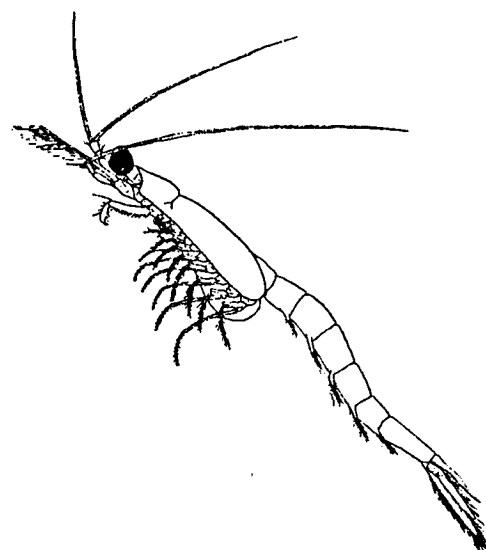


Figure 21 Mysid or opossum shrimp, often 8-12 mm. (modified from Pennak 1953)

have shown that the optimal salinity for this species is near 10‰, at which it is never found in great numbers, while the salinities at which it occurs in its greatest densities (1-4‰) are remarkably osmotically stressful (Sitts 1978).

The upstream limits of *N. mercedis* abundance appear to be set partly by light intensity. Fifty percent or more of the adult population is found at depths where light intensity is less than 10-5 lux (Heubach 1969). In most Delta waters depths must be greater than 3 m to provide sufficient attenuation of sunlight. In areas where the channels are not at least 3 m deep, *N. mercedis* is absent (Heubach 1969). Similarly, in channels with shallow sides, *N. mercedis* is found only in the deeper, central parts of the channel. These conditions are probably one reason for the greater abundance of *N. mercedis* in the deeper stations (Heubach 1969). At night these patterns of shrimp abundance in relation to depth break down and *N. mercedis* is found uniformly distributed throughout the water column (Heubach 1969; Sitts 1978; Siegfried et al. 1979). Siegfried et al. (1979) used a smaller mesh net than earlier studies, which permitted them to catch representative numbers of young shrimp. They found that shrimp less than 3 mm long did not seem to respond as strongly to light intensity as larger shrimp, so that small shrimp were common in the upper parts of the water column (they may even be positively phototactic).

Net flow velocities greater than 0.12 ms⁻¹ appear to prevent *N. mercedis* from maintaining its position in a channel (Turner and Heubach 1966; Orsi and Knutson 1979) and, thus, are barriers to the upstream migration of the shrimp. Operation of the cross-delta channel in 1974 provided evidence of the importance of net flow velocity (Turner and Heubach 1966). Before the gates to the channel were opened flows, in the Sacramento River at Isleton were lower than 0.12 ms⁻¹, and flows in the cross-channel were less than 0.12 ms⁻¹; *N. mercedis* were absent from the Sacramento River and present in the Mokelumne River. After the gates to the channel were opened the flow rates switched between the two sites, as did the distribution of *N. mercedis*. Looking throughout the Delta, Turner and Heubach (1966) found that *N. mercedis* were seldom found in channels with net flows over 0.12 ms⁻¹. During the drought of 1976-77 the barrier effects of net flow were weakened by the greatly reduced outflows and, as a consequence, *N. mercedis* were found much further upstream than usual (Knutson and Orsi 1983).

In addition to their diel vertical migrations in response to light, *N. mercedis* also migrate in response to tidal flows. Adults tend to remain on the bottom during ebb tides and rise into the water column during flood tides. Combined with the landward-flowing, density-driven current on the bottom, this behavior tends to move the adult shrimp up into the more freshwater parts of the estuary (Orsi and Knutson 1979; Siegfried et al. 1979). The greater occurrence of young shrimp near the surface of the water column tends to move them downstream from the adults and into the entrapment zone (Siegfried et al. 1979; Orsi 1986). The entrapment zone also concentrates nutrients, phytoplankton, and suspended detritus (Arthur 1975; Ball 1975; Arthur and Ball 1979), making it an ideal nursery area for *N. mercedis* (Siegfried et al. 1979). The results of Siegfried et al. (1979) suggest that young *N. mercedis* would continue to be carried by surface currents on through the entrapment zone.

and down to the sea. However, substantial numbers do maintain themselves above the entrapment zone.

Studies through several years (Orsi 1986) indicate that there is less of a difference in vertical migration between different ages of *N. mercedis* than reported by Siegfried et al. (1979), whose study encompassed only one year. Smaller individuals are more likely to migrate into the more lighted surface waters on flood tides, when they would be carried upstream. The greater occurrence of smaller *N. mercedis* in landward-flowing flood tides explains their observed scarcity in waters seaward of the entrapment zone. Seaward of the entrapment zone, greater water clarity allows deeper light penetration and most *N. mercedis* of all sizes are in the landward-flowing, bottom, density current. Within the entrapment zone, water clarity is low and most of the population moves up into the area of neutral flow between the surface, river outflow layer and the deeper density-driven currents.

Neomysis mercedis undergoes extremely large seasonal fluctuations in abundance, from mean densities in winter of less than 10m^{-3} to almost $1,000\text{m}^{-3}$ in spring. Three main bouts of reproduction occur each year, but the high densities of late spring overlap the smaller peaks (Siegfried et al. 1979). The overwintering population consists mostly of large, adults which breed in the early spring. The first generation of the year grows at the same time as the populations of phytoplankton are multiplying. Fecundity is directly related to size, but females in late spring produce more young than females of the same size in early spring (Heubach 1969). Reproduction by the early spring generation produces the large concentrations of *N. mercedis* in late spring. In addition to the changing relationship of length with fecundity, *N. mercedis* matures at smaller sizes in summer than in winter or spring. The summer population produces the overwintering generation.

High temperature (Heubach 1969; Siegfried et al. 1979), low dissolved oxygen (Turner and Heubach 1966; Orsi and Knutson 1979), predation (Heubach 1969), and seasonal declines in temperature and phytoplankton (Orsi and Knutson 1979) have all been suggested as the force behind the fall decline in *N. mercedis* abundance. Hair (1971) found that the upper lethal temperature limit for *N. mercedis* was $24.2\text{--}25.5^{\circ}\text{C}$, although levels of dissolved oxygen can apparently affect the degree of stress caused by high temperature (Orsi and Knutson 1979). In the San Joaquin River at Stockton, near-lethal temperatures are combined with low dissolved oxygen, and it may be the combination, rather than either factor alone, that decimates that population (Orsi and Knutson 1979). Heubach (1969) observed that the greatest numbers of young striped bass, which eat primarily *N. mercedis*, are in the same area as their prey but was unable to quantitatively test this hypothesis because he had no measure of bass abundance.

The diet of *N. mercedis* varies by size, through time, and by location within the estuary. Larger individuals usually prefer copepods, particularly *Eurytemora affinis*, while smaller individuals ($<3\text{ mm}$ total length) primarily consume phytoplankton and rotifers (Baldo Kost and Knight 1975). Like most mysids (Mauchline 1971; Foulds and Mann 1978), *Neomysis mercedis* is primarily a filter-feeder, taking what passes through its filtering

current, rather than chasing individual items. However, there is clear selection of the material ingested from that caught on the filter pads. When rotifers are abundant, the juvenile *Neomysis* take more of them, and the juveniles probably derive most of their energetic gain from that part of their diet (Siegfried and Kopache 1980). Even among the phytoplankton species, whose energy contents are much less than those of animal material, there is strong evidence of selection. From March to May 1976, *Skeletonema* was by far the dominant diatom in the western Delta, but the guts of *Neomysis* contained mostly *Melosira* or *Thalassiosira*. Similarly, from June to November the only common diatom in gut samples was *Thalassiosira* although it was a very small part of the phytoplankton assemblage present. Larger individuals fed primarily on zooplankton and showed strong prey selection. Copepod nauplii were the most abundant component of the zooplankton assemblage but were rarely consumed. *Neomysis* guts predominately contained *Eurytemora affinis*, harpacticoid copepods, and rotifers (Siegfried and Kopache 1980).

Annual abundance of *N. mercedis* for the July to October period can be accurately predicted from knowledge of chlorophyll *a* concentrations and either of the interconnected variables of salinity at Chipp's Island or Delta outflows (Orsi and Knutson 1979). Studies during the drought of 1976-77 (Siegfried et al. 1979) suggested that the location of the entrapment zone determines the annual fluctuations in *N. mercedis* abundance. If the entrapment zone is in the deep channels of the main rivers, as happens when delta outflows are low, then chlorophyll *a* concentrations remain low. When outflows are higher, salinity at Chipp's Island is lower, and algal populations accumulate in the broad shallows of Suisun Bay. Presumably, this relationship between the location of the entrapment zone and *N. mercedis* abundance is increased food supplies (mainly copepods which feed on the algae) for the shrimp when the zone is located in Suisun Bay. Regression analysis of the abundance of *N. mercedis* from 1968 to 1981 indicates that, in addition to outflow, the abundance of the copepod *Eurytemora affinis* is significantly linked to the density of adult *N. mercedis* (Knutson and Orsi 1983).

All of the factors associated with low abundance of *N. mercedis* have been unfavorable in recent years: low outflow, high salinity at Chipp's Island, low chlorophyll *a* concentrations in Suisun Bay, greater water clarity, and low densities of *E. affinis*. Under the conditions in Suisun Bay, it is not surprising that populations of *N. mercedis* have been lower for almost all years of the 1980s than in earlier years. The hypothesis that the population was limited by predation appears unlikely because most fish species which feed on *N. mercedis* have simultaneously declined in abundance. However, the current practice of introducing large numbers of hatchery-reared juvenile striped bass into the Delta may provide a test, albeit intentional, of this hypothesis.

Outflow, as one of this linked set of variables, is a partial predictor of *N. mercedis* abundance (CDF&G 1987b) and periods of drought in the late 1970s and 1980s coincide with the lowest recorded densities of the shrimp but the relationship is not simple (Siegfried et al. 1979; CDF&G 1987b; Figure 22). Exceptionally high outflows appear to have carried *N. mercedis* out of their normal habitat, likewise drought periods coincide with very low *N.*

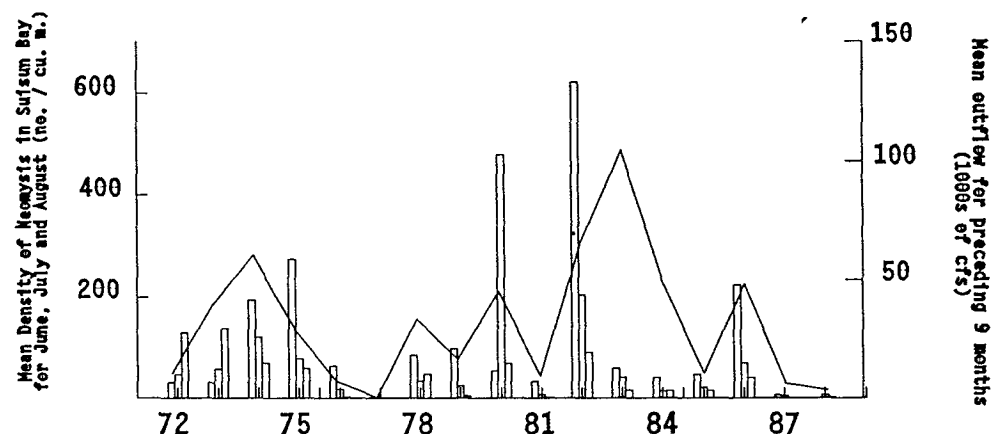


Figure 22 Abundance of *Neomysis mercedis* in July, August, and September (bars) in comparison to previous mean outflow rates (line). Data from CDF&G and DAYFLOW.

mercedis densities. In intermediate years, higher outflows that are to be associated with lower salinities in Suisun Bay and the western Delta and with higher concentrations of chlorophyll *a* seem to support larger populations of the opossum shrimp. However, other factors seem to have controlled abundance of *N. mercedis* in recent years of moderately high outflow, because occasional peaks in abundance occur during a period of general decline. It is worth noting that in the first years of the study abundance increased through the summer months, which was also the pattern in 1963 (Turner and Kelley 1966). Since 1974, the peak abundance of *N. mercedis* has occurred earlier and rapidly declined through the summer.

The recent effects of drought on *N. mercedis* have been exacerbated by the extremely low levels of chlorophyll *a* in Suisun Bay since the establishment of *Potamocorbula amurensis*. The different mechanisms presumed to affect *N. mercedis* abundance are probably all contributing to the low densities observed:

1. Lower outflows restrict the entrapment zone to deeper, more upstream channels which are less likely to promote high densities of *N. mercedis* (CDF&G 1987b).
2. Lower outflows produce weaker landward currents along the bottom so that the ability of *N. mercedis* transported downstream to return to the entrapment zone is reduced.
3. *Eurytemora affinis* abundance has remained consistently low through recent years.
4. Larger numbers of *N. mercedis* may be exported through the CVP and SWP pumps as a result of the increased proportion of inflow diverted during drought years. The location of the entrapment zone within the lower river channels during dry years (Siegfried et al 1979) increases the vulnerability of *N. mercedis* to such displacement.

N. mercedis populations have not shown the sort of consistent declines shown by most other elements of the zooplankton. Despite increasing frequencies of low levels, the trend

rough time is not significant because the population has occasionally rebounded to high densities (CDF&G 1987b; Orsi et al. 1991).

4.5.2.4 Other Crustacea

A number of other types of crustacea have been collected in the course of sampling plankton in the estuary. Oceanic species of krill (Euphausiidae) enter the Bay in greater numbers when outflow is high, probably as a result of *El Niño* effects or the greater strength of bottom currents (CDF&G 1987d). The three most commonly collected species are *Stomatodes difficilis*, *Thysanoessa gregaria*, and *Nyctiphanes simplex*. Central Bay is usually the only area where these shrimp occur in abundance, but during periods of high outflow they have been found in channel stations up to Carquinez Straits and the far south end of South Bay (CDF&G 1987d). *N. simplex* is normally found south of Point Conception but appears to have been brought further north by *El Niño* conditions in 1983.

Larvae of the ghost shrimp (*Callinassa californiensis*) are also a common feature of the zooplankton in Central Bay, but they are much less common elsewhere (CDF&G 1987). Young larvae appear to be carried out of the Bay in the surface water by high flows, and older larvae enter the Bay on bottom currents. The net effect of high outflow is to reduce the abundance of ghost shrimp larvae because the number transported out of the Bay by high outflows is greater than that carried in by the consequently stronger bottom currents. Years of low outflow cause more of the shrimp larvae to remain in the Bay, and larval populations are therefore higher. Because the status and dynamics of the adult population is entirely unknown it is impossible to say whether the greater retention of small larvae in the Bay during dry years produces a larger adult population than the greater immigration of larger larvae into the Bay in wet years (Strathman 1982).

In Suisun Bay, and to a much lesser extent San Pablo Bay, larvae of the introduced pea crab *Rithropanopeus harrisi* are caught in plankton samples. Adults are known to occur as far upstream as Stockton but breeding must occur in salt water (Barnes 1980). *R. harrisi* was first reported from the estuary in 1940; how it was transported from its native range along the Atlantic coast is unknown. High summer outflow, when the larvae are planktonic, is inversely correlated with larval abundance (CDF&G 1987).

4.6 Benthos

As with the fish, the aquatic invertebrates of San Francisco Bay are a mixture of native and introduced species, with introductions outnumbering natives in most areas and habitats (Nichols 1979; Nichols and Thompson 1985a, see Nichols and Pamatmat 1988 for detailed descriptions). In large part the dominance by many introduced species is a reflection of what appears to have been a depauperate native fauna. Carlton (1979) quotes William Stimpson's observation in 1857 that "The Bay of San Francisco ... is nearly barren of animal life except at its entrance." However, contemporary observations on the abundance of native oysters in South Bay paint a very different picture (Skinner 1962). In 1979, almost 100 species of introduced invertebrates could be catalogued (Carlton 1979). Since then more species have entered the ecosystem and have led to complete changes in community structure of the zooplankton and benthos, particularly in Suisun Bay and the western Delta.

New species arrive in the estuary through two major modes: as part of the transport of economically valued importations (principally oysters and their symbionts), and as part of a fouling community on and in ships. More rigid regulations and greater awareness of ecological impacts have led to a slowing in the rate of intentional importation. Ironically, the eastern oyster *Crassostrea virginica* never became established in San Francisco Bay but dozens of its symbionts did. Larger ships, and the use of cargo canisters, have increased the quantity of water carried as ballast, and most recent introductions have arrived without intentional human help. The economic and ecologic impacts of many of these species have been profound, destroying pilings, weakening dikes, fouling drainpipes, and blocking water canals, as well as reducing the availability of food for higher trophic levels.

Most benthic organisms in the Estuary, especially in San Francisco Bay, are introduced species. They arrived as hitchhikers with oysters, attached to ship bottoms, and in ballast water. Most of the species came from polluted bays and estuaries and survived long sea voyages, so are very hardy. As a result, a cosmopolitan fauna of hardy estuarine organisms is developing, typified by the organisms in San Francisco Bay.

The factors most affecting the abundance, composition, and health of the benthic community from year to year are outflow from the Sacramento-San Joaquin Delta, local runoff, and pollution (Nichols and Pamatmat 1988). The importance of pollution in controlling benthic communities has been assumed to be very high because several fisheries disappeared from South Bay as the city of San Francisco grew (Skinner 1962). In the modern estuary the water flow and pollutional loads are linked through increased concentration and mobilization of toxics. Lower outflows are also associated with lower phytoplankton biomass and hence lower productivity during periods of low flow in parts of the Bay complex. High outflows lead to lower salinities, which particularly control the species abundance and composition in shallow areas where animals are exposed to less saline surface waters.

The benthic community shows strong response both to seasonal changes of the environment and to aperiodic changes from year to year. Recruitment rates change in most species in response to salinity, temperature, and a variety of other environmental conditions; but migration of animals to other parts can confound studies of the effects of environmental effects on recruitment (Nichols and Thompson 1985b).

4.6.1 Molluscan Fisheries

4.6.1.1 Oysters

Native oysters (*Ostrea lurida*; Figure 23) had always been extremely abundant in South and Central bays, based on the extensive build-up of shells in these areas. Middens of the California Indian tribes include large accumulations of oysters, even within the Delta where they must have been carried in trade (Skinner 1962; Hedgpeth 1979; Nichols 1979). The flavor of these oysters was disdained by European settlers and led to the first importations of foreign species into the Bay. In the latter half of the 19th century large quantities of eastern oysters were introduced and supported a large landing in the Bay Area. The eastern oyster never successfully reproduced in the Bay, so seed oysters were constantly needed. Transportation of eastern oysters also introduced the predatory eastern oyster drill and the new predator may have played a large role in initial declines of the native oysters (Smith and Kato 1979). Oyster landings declined from 1915 but importation of Pacific oysters (*C. gigas*) from Japan boosted production after its introduction in 1930. Like the eastern oyster, the Bay Area harvest rested on constant importation of new seed oysters, so World War II brought an end to Pacific oyster culture in the Bay (Skinner 1962).

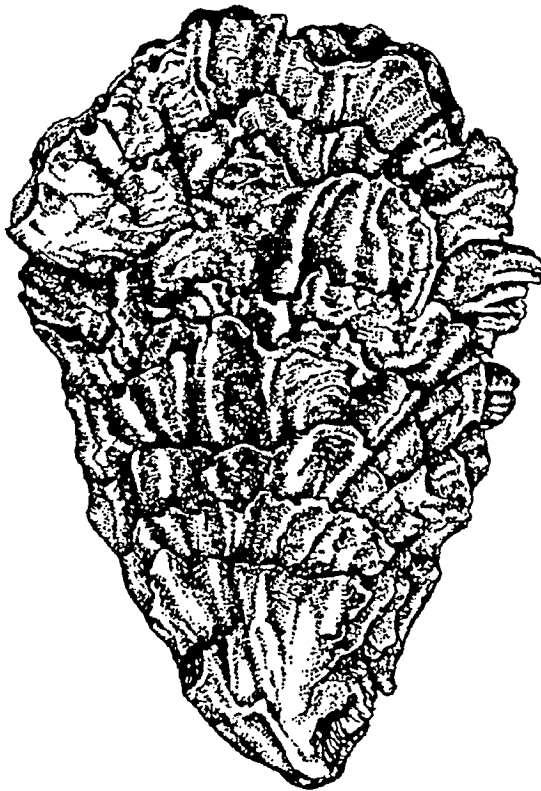


Figure 23 Pacific oyster, 10 cm. (Modified from Emmett et al. 1991.)

4.6.1.2 Clams

All but two of the common benthic molluscs of the modern Bay are introduced (Nichols and Pamatmat 1988; Table 1). Within the Delta the dominant mollusc is the Asiatic clam, *Corbicula fluminea*, which is intolerant of saline waters while the clams of the Bay are

intolerant of freshwater. Until recently the seasonal shifts in salinity reduced the clam populations in Suisun Bay except during periods of extended drought, as in 1977 when large concentrations of softshell clams, *Mya arenaria* (Figure 24), occurred (Nichols 1985).

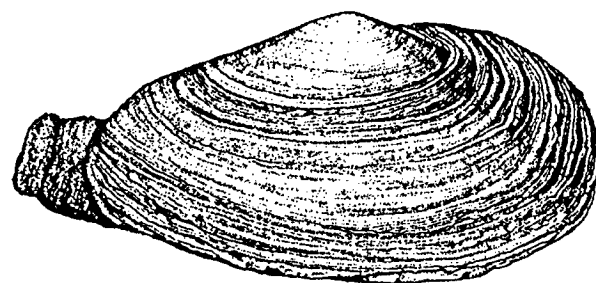


Figure 24 Softshell clam, *Mya arenaria*, 10 cm. (Modified from Emmett et al. 1991).

Clam fisheries in the Bay originally were based on dense populations of the bent-nose clam (*Macoma nasuta*) and the bay mussel (*Mytilus edulis*). Following importation of the Atlantic soft shell clam (*Mya arenaria*) with shipments of oysters in 1869, the bent-nose clams largely disappeared. Harvest rates of soft shell clams were heavy: from 1889 to 1899 landings from the bay ranged from 500 to 900 tons. Overharvest, habitat loss, and increasingly severe pollution were probably the most important factors causing the soft shell clam landings to decline to 245 tons in 1916, 68 tons in 1927 and none by 1949. Partially contributing to the decreasing take of soft shell clams may have been the increasing harvest of Japanese littleneck clams (*Tapes japonica*) that were introduced with Pacific oysters during the 1930s. Pollution led to extremely high bacterial concentrations in the Bay, and from 1932 to 1953 there was a general quarantine on shellfish from the Bay. Improved water quality in recent years has led to larger sport shellfishing on the large populations of mussels and softshell and littleneck clams that now exist in the Bay (McAllister and Moore 1982). The harvested bivalves are used both as human food and as bait for sportfish.

Table 1. Molluscs of the San Francisco Bay and Delta, based on Carlton 1979, and Gleason 1984.

Species	Year of First Description
<i>Mytilus edulis</i>	Native
<i>Macoma balthica</i>	Native (?)
<i>Ovatella myosotis</i>	1871
<i>Mya arenaria</i>	1874
<i>Urosalpinx cinera</i>	1890
<i>Gemma gemma</i>	1893
<i>Ischadium demissum</i>	1894
<i>Crepidula convexa</i>	1898
<i>Crepidula plana</i>	1901
<i>Ilyanassa obsoleta</i>	1907
<i>Teredo navalis</i>	1913
<i>Hydrobia ulvae</i>	1920
<i>Petricola pholadiformis</i>	1927
<i>Busycotypus canaliculatus</i>	1938
<i>Mytilus senhousia</i>	1945
<i>Corbicula fluminea</i>	1946
<i>Mytilus japonica</i>	1946
<i>Littorina littorea</i>	1968
<i>Theora fragilis</i>	1982
<i>Potamocorbula amurensis</i>	1986

The most recently introduced member of the assemblage appears to be an indirect result of opening up trade with the Chinese mainland, the new Asian clam *Potamocorbula amurensis*. This mollusc was not discovered in the bay until 1986 but by 1987 and 1988 had achieved densities of up to 30,000 m⁻² and was distributed throughout Suisun Bay and in parts of South Bay in salinities from 1 to 33‰ (Carlton et al. 1990). In Suisun Bay the previous association of benthic species largely disappeared as *Potamocorbula amurensis* multiplied. The invader had an advantage by appearing after a tremendous storm in February 1986 had removed most of the normal benthic animals (Nichols et al. 1990). Since the establishment of *Potamocorbula amurensis*, normal summertime phytoplankton blooms have failed to occur and chlorophyll *a* densities have remained at some of the lowest values recorded. The short time which has elapsed since the almost complete conversion of the former diverse, fluctuating benthic community into the present, spreading monoculture of the Asian clam precludes any confident guesses on the long-term effects of the clam on other biotic resources of the Bay (see Appendix A).

4.6.2 Crustacean fisheries

Unlike the molluscs, the epibenthic crustacea are still made up of many native species, particularly young Dungeness and other, smaller crabs as well as crangonid shrimps. Introduced species include the small Asian crab *Rhithropanopeus harrisi* and the Korean shrimp *Palaemon macrodactylus*. In the upper Bay complex the epibenthos consists entirely of introduced species, particularly the crayfish *Pacifasticus leniusculus* which were introduced from Oregon in 1898. The red swamp crayfish, *Procambarus clarki*, is also widely distributed in the Delta. Other estuaries on the Pacific coast from Alaska to Baja California contain the blue mud shrimp, *Upogebia pugettensis*, and the ghost shrimp, *Callinassa californiensis*. These burrowing shrimps are sold as live bait in the Bay but there is no description of their adult populations or distributions in the Bay. Larvae of *C. californiensis* are a part of the zooplankton community below Carquinez Straits (CDF&G 1987d).

The benthic epifauna, except for Dungeness crabs (*Cancer magister*), are probably the least studied community of animals of the Sacramento-San Joaquin estuary.

4.6.2.1 Dungeness Crab

The most familiar member of the benthic community is the Dungeness crab, *Cancer magister*. For the first sixty years of this century, Dungeness crabs were an increasingly important fishery for San Francisco. Landings rose from 1-2 million pounds in the years before 1925, to 3-4 million pounds for most years between 1925 and 1945, and finally to 4-8 million pounds in most years from 1945 to 1959 (Skinner 1962). Changing oceanic conditions in 1959 caused the population and catch of crabs to drop dramatically. Some crabs were harvested within the Bay before 1900 but since then all landings have been from crabs caught outside the Golden Gate.

The absence of adult crabs, and hence a fishery for them, in San Francisco Bay has tended to obscure the abundance of this animal in the Bay; the potential of the Bay as a nursery area has been clearly shown (Tasto 1983a,b). As much appropriate nursery habitat exists in the Bay as in the Gulf of the Farallones (500 km²) with much variability in the size of the Bay contribution to the coastal adult population (Tasto 1983a).

Dungeness crab reproduction takes place entirely at sea (Figure 25). Fertilized eggs are retained by the female on her abdominal appendages. Ovigerous females are first found in the Gulf in late September, and the peak of spawning occurs during October and November (the following description is based on Reilly 1983). By January most eggs have hatched, and the zoea larvae enter the water column. Eggs apparently hatch earlier in warmer years, and most hatching occurs within a two-week period, the timing of which shifts from year to year. However, some of the population continues to produce new zoea as late as mid-May. Zoea larvae of Dungeness crab are the most abundant crab larvae in areas where depths exceed 3 m. The zoea show strong diurnal migrations to the surface during the night and to 25-30 m

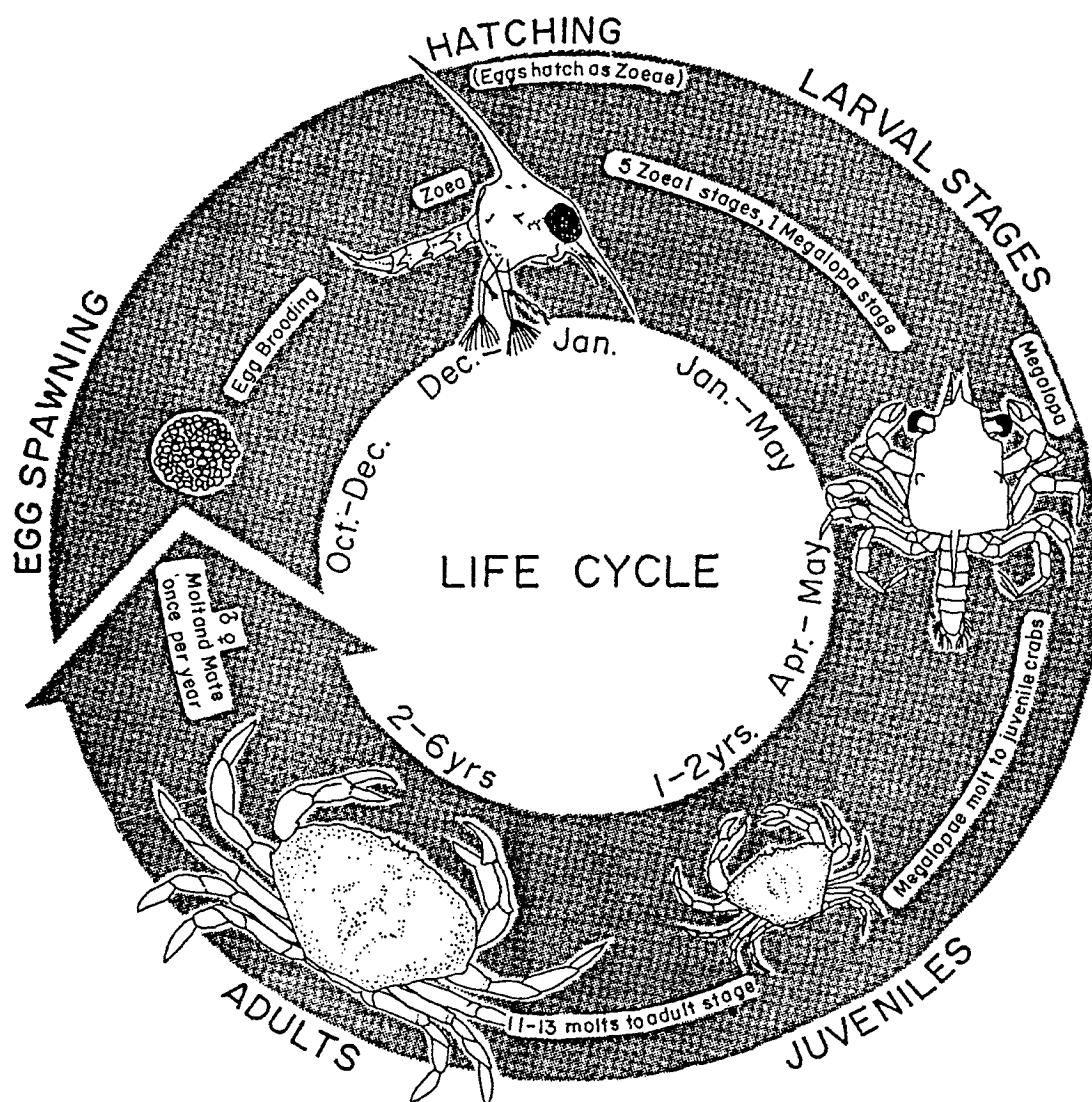


Figure 25 Life cycle of Dungeness crab in California (from Tasto 1983)

during the day. The zoea also are absent from salinities below 32‰. Because of this sensitivity to low salinities, the freshwater plume from the Golden Gate plays a large role in determining the distribution of early zoeal stages during years of high outflow (Hatfield 1983a). Zoeal stages III through V are almost absent from the Gulf of the Farallones.

After five molts the zoea transform into more crab-like larvae called megalops. Transformation to megalops begins to occur in late March or April. Megalop larvae appear to cease the diel migrations of the zoea and are found within 15 m of the surface at all hours. Megalops also differ from zoea in their preference for shallow water. Transformation of the zoea coincides with the weakening of the Davidson Current and the switch to upwelling conditions. The mechanism for transporting megalops toward the coast is unclear, but it may be associated with changes in surface flow patterns either by gyres formed behind counter-clockwise gyres south of headlands or by transitory shifts in wind direction (Hatfield 1983a; Reilly 1983). However they get there, the mouth of San Francisco Bay is a major settling area (Hatfield 1983b). Dungeness crabs enter San Francisco Bay only as juveniles, molt into the new form after 25 to 30 days as megalops (Hatfield 1983b).

The number of crabs entering the Bay is primarily a function of megalop abundance and perhaps, the strength of the landward flowing bottom current (Tasto 1983). High outflows also appear to reduce the transport of crabs into the Bay. From 1980 to 1989 otter trawls May to June, throughout the Bay, showed much lower abundances in 1983 and 1986, two years with the highest outflows ever recorded. Dungeness crabs attained higher abundance in the Bay in years following these 'washouts,' than they had prior to them. Note that high outflows are frequently associated with *El Niño* events and other oceanic conditions that are suspected of reducing megalop abundance. Overall the abundance of crabs in the Bay has continued to vary widely through the ten years of the Bay Study, without showing any obvious trend and with quite different measures of abundance from different sampling methods (Herrgesell 1990).

Dungeness crabs enter the Bay during May or June and leave the Bay by August or September of the following year when their carapace width is 90-120 mm (Collier 1983). Larger crabs (carapace widths greater than 100 mm) have growth rates which are significantly slower than smaller juvenile (20-100 mm carapace width; Collier 1983). The slowing in growth rates coincides with the onset of sexual maturity in the male and the beginning of emigration from the Bay. There is also an unexplained significant difference in growth rates among years (Herrgesell 1990); which is most apparent for years of high abundance. Growth rates of juvenile crabs in the Bay is much higher than in offshore areas: growth rates off Bodega yield crab widths of only 45 mm at one year of age compared to an average of 102 mm for year old crabs in the Bay (Collier 1983). Thus, the use of the Bay as a nursery area permits much more rapid attainment of sexual maturity (Wild et al. 1983). The Bay population contributes as much as 83% of the crabs of the Central California fishery (Tasto 1983a).

Dungeness crabs are particularly abundant from Richardson's Bay upstream through Suisun Bay, showing greater abundance upstream in years of low outflow (Tasto 1983b). Crabs are found where bottom salinities are less than 10.2 ‰, and the onset of high outflow from winter storms results in a mass movement of crabs to more downstream locations. San Pablo Bay is the area of most consistently high numbers of juvenile Dungeness crabs.

Emigration from the Bay by year-old crabs is influenced by carapace width and outflow so that in years of slower growth or lower delta outflow crabs remain in the Bay longer. In general Dungeness crabs leave the Bay by August or September of the year following their arrival; so only one year class is present for most of the year, except for summer when newly settled crabs have just arrived and the older juveniles have not yet emigrated (Collier 1983). Due to the common occurrence of cannibalism in decapods a year of slow-growing, abundant juveniles may reduce the subsequent year class size.

Periodicity of Dungeness crab landings is more apparent off the Northern California coast Bay than in fishing grounds to the north (Figure 26). The cause of this periodicity has been suggested to be periodic shifts in upwelling (Peterson 1973, rebutted by Botsford and Wickham 1975), cannibalism by older crabs on younger juveniles or through a predator/prey cycle with an egg-eating worm (Botsford and Wickham 1978; possible role of cannibalism argued in McKelvey et al. 1980 vs Botsford 1981). Switching in fishing effort from salmon to crabs by fisherman, and its consequences on predation effects of salmon on crabs, has also been entertained and dismissed (Botsford et al. 1982).

MILLIONS OF POUNDS

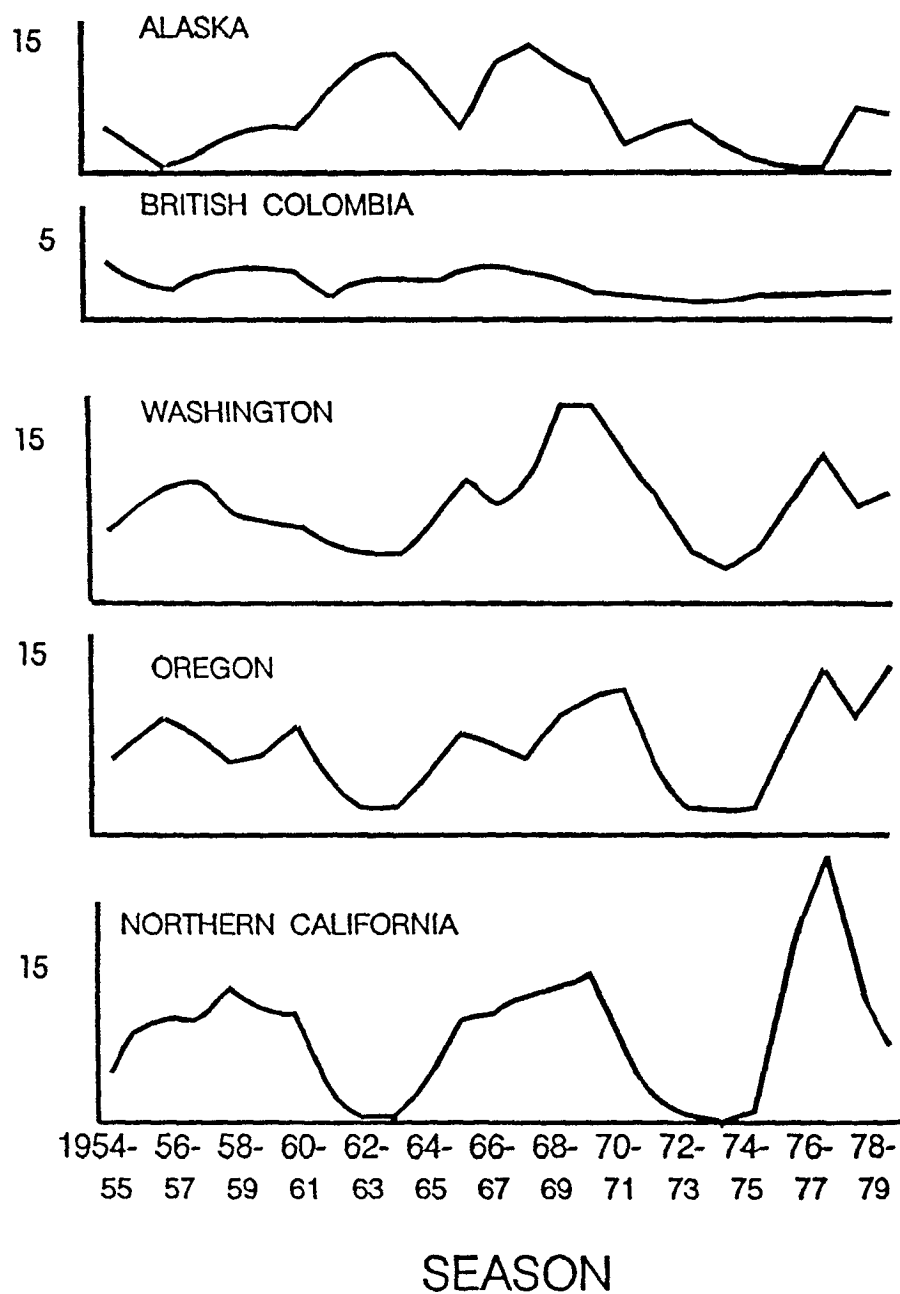


Figure 26 Crab catch in different areas of the Pacific coast fishery. Data from T 1983.

A decline in Dungeness crab catch overall through the 1960s and 1970s has been clearly linked to an increase in ocean water temperatures (Huang 1972; Namias and Huang 1972; Wild et al. 1983). After 1959 mean ocean temperature near San Francisco Bay rose by about 1 C relative to the preceding period of record, the crab catch from four years later sharply declined and has stayed at consistently lower levels than occurred previously (Figure 27).

The abundance of the first zoeal stage is inversely related to temperature, with the highest densities recorded during the coldest winters. Size of the adult population is also apparently a major determinant of zoeal abundance.

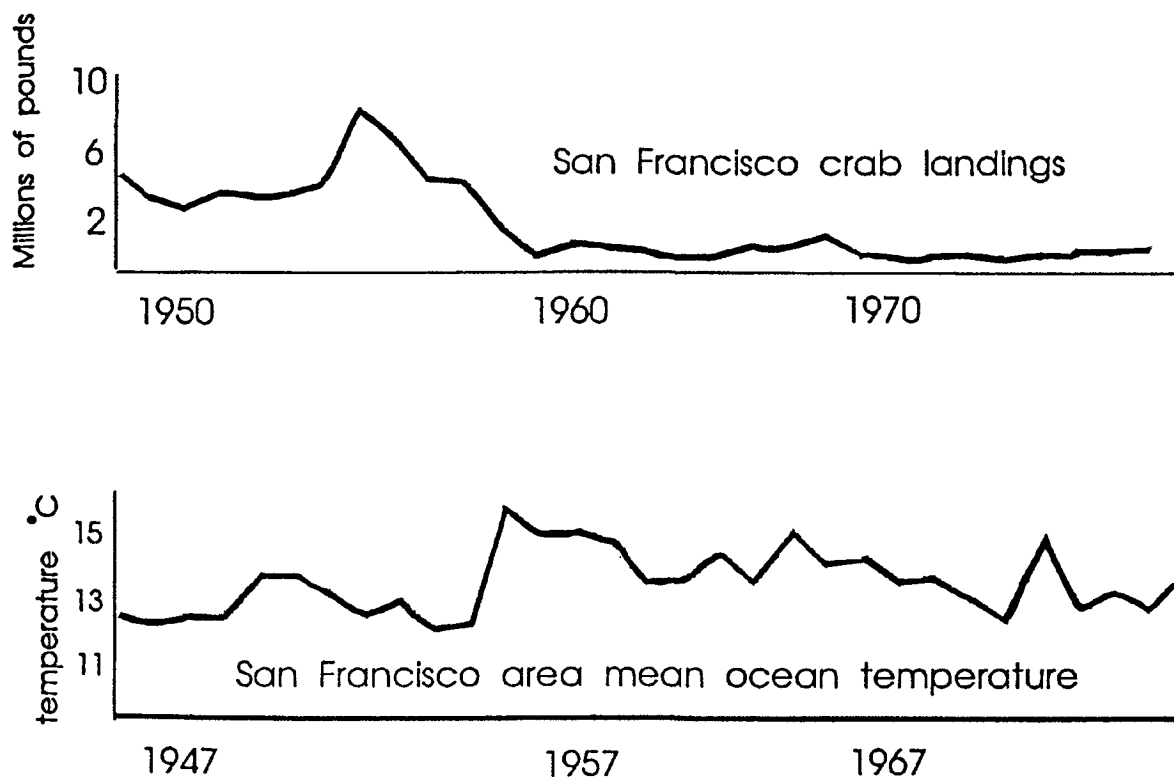


Figure 27 Landings of Dungeness crabs at San Francisco compared to mean ocean temperatures four years previously when the harvested crabs would have been planktonic larvae (modified from Wild et al. 1983).

There is little association between zoeal abundance and megalop abundance but megalop abundance is strongly tied to subsequent juvenile crab abundance. Thus, whatever controls zoeal survival in the ocean is probably the strongest control on crab abundance (Tasto 1983a).

4.6.2.2 Shrimp

The smaller epibenthic fauna in the Bay is dominated by four species (*Crangon franciscorum*, *C. nigricauda*, *C. nigromaculata*, and *Palaemon macrodactylus*) commonly called grass shrimp by anglers and bait sellers (Figure 28). These species of shrimp seldom exceed 70 mm in total length. They are not used as food by most U.S. citizens, who are accustomed to eating much larger shrimp. However, San Francisco Bay is the only North

American estuary to have developed a major fishery for these small, crangonid shrimp. In 1869, Italian immigrants collected shrimp in seines and sold them as food. The fishery shifted to the newly arrived Chinese community in 1871 because they brought better techniques and more efficient, stationary nets that caught shrimp during falling tides (Scofield 1919; Skinner 1962). The shrimp were mostly dried and exported to China. Annual landings from 1882-1892 averaged 2,270 tons but the fishery was resented by the harvesters of finfish, who objected that the nets killed large numbers of juvenile fish. Increased regulation and, probably, decreased abundance due to overharvest caused average catches to decline in through the turn of the century to only 200 tons in 1916. Through the 1920s and 1930s annual catch rose to an average of 1000 tons with a maximum harvest in 1935 of 1591 tons (CDF&G 1987b). Political upheaval in China led to abandonment of the California export fishery in the late thirties. Discovery of offshore populations of shrimp and prawns in 1952 shifted the remaining fishery out of Bay waters (Skinner 1962). In 1965 a Bay fishery for shrimp was reestablished to provide bait for striped bass and sturgeon fishers. The bait fishery takes approximately 68 to 91 tons of shrimp each year from the Bay (Siegfried 1989).

C. franciscorum (California bay shrimp) are most abundant in lower salinities with young being found in almost fresh water, *C. nigricauda* (blacktail bay shrimp) prefer salinities of 25‰ or more, and *C. nigromaculata* (blackspotted bay shrimp) are seldom found at salinities below 30‰ (CDF&G 1987b). Ovigerous females of all species migrate to higher salinity water to release their eggs. Newly hatched zoea swim to the upper water column and are carried further downstream by outflowing surface waters (Sitts 1978). Later zoeal stages are found in lower parts of the water column and, so, are transported into the bay from offshore regions by bottom currents (Siegfried et al. 1978; Hatfield 1985). The distribution of *C. franciscorum* is also tied to the distribution of its most common food item, *Neomysis mercedis*, with more crangonids found where *N. mercedis* is concentrated and also showing higher feeding rates in such areas (Siegfried 1982). Diets of the species are quite variable, shifting in association with the array of prey available, with the size of the individual, and in accord with the different salinity/temperature preferences of the species (Wahle 1985). *C. franciscorum* and *C. nigricauda* are found along all of the California coast,

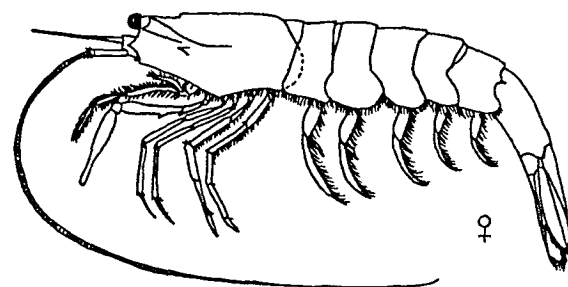


Figure 28 *Crangon franciscorum* (from Smith and Carlton 1975)

but San Francisco Bay represents the northernmost tip of the range of *C. nigromaculata*. These shrimp are common food items for many fishes of the Bay and Delta, including: striped bass, American shad, green and white sturgeon, white catfish, and Pacific tomcod (Ganssle 1966).

The other abundant shrimp, *Palaemon macrodactylus*, was introduced from Korea (Newman 1963). *P. macrodactylus* is found only in the upper estuary, particularly Suisun Bay, Suisun Marsh, and the western Delta.

All three *Crangon* shrimps captured by the Bay Study show obvious responses to flow patterns (Figure 29; based on Herrgesell 1990). The tightest, and simplest, correlation is between the log-abundance of *C. franciscorum* abundance with the log of outflow ($r=.91$ for the period 1980-1988). The mechanism appears to be greater transport of post-larval shrimp into the Bay by bottom currents in years of high outflow. Greater amounts of lower salinity water also probably play an important role by providing suitable nursery habitat (CDFG 1987b; Herrgesell 1990). *C. nigricauda* and *C. nigromaculata* also showed sharp increases in abundance in years of higher outflow; however, both species have maintained higher populations in the Bay during the drought years following the high outflows of 1986, while *C. franciscorum* has returned to low levels characteristic of other years of low outflow. The decreased food abundance in Suisun Bay in recent years (Appendix A) may also have played a role in reducing the abundance of *C. franciscorum* since it is the only crangonid to be found in abundance that far upstream. As a consequence of these differences in response to drought, in 1988 abundance of *C. nigricauda* exceeded that of *C. franciscorum* for the first time. A less abundant species, *Heptacarpus* is also apparently favored by higher salinities in the Bay since it increased in 1987-1988 to three times the abundance it had shown in earlier years. The introduced *Palaemon macrodactylus*, despite a distribution tied to lower salinity water, shows no apparent change in abundance with outflow. This species is more often found in association with emergent vegetation in shallow water and may not be as effectively sampled by trawls.

The interaction of direct effects of outflow on shrimp abundance with the indirect effects of outflow on their principal prey and predators could make it difficult to predict their future abundance (Armor and Herrgesell 1985). However, to date, *C. franciscorum* exhibits a straightforward response to outflow alone, and the other species appear to respond more to Bay salinity.

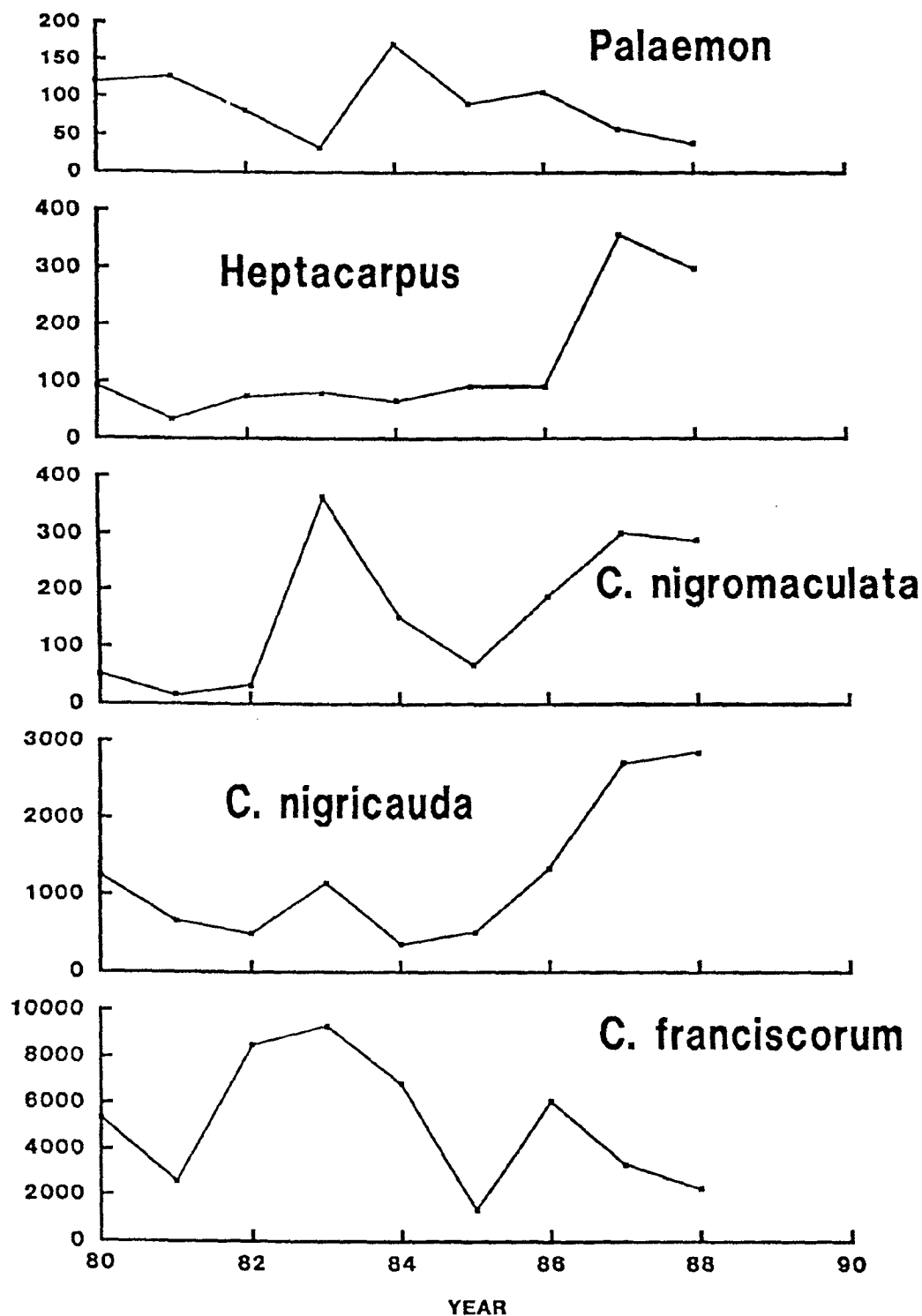


Figure 29 Abundance indices of 5 species of shrimp in otter trawls of the Bay Study 1989 (data from Herrgesell 1990).

4.6.2.3 Crayfish

Crayfish are harvested both commercially and for sport from waters of the Delta (Kimsey et al. 1982). The only native crayfish of the estuary, the sooty crayfish (*Pacifasticus nigriscens*), was harvested from Coyote Creek in large numbers in 1870 for consumption in San Francisco (Steinhart 1990). The population was eradicated before the turn of the century, apparently by the introduction of the signal crayfish, *P. leniusculus*, (Kimsey et al. 1982). There does not seem to have been any native crayfish in the Central Valley between the Shasta crayfish on the Pit River and the sooty crayfish around South Bay.

Signal crayfish were first found in California in San Francisco in 1898 (Kimsey et al. 1982). Signal crayfish prefer cool waters and are tolerant of salinities up to 17 ‰. Signal crayfish do not burrow and, so, are found most abundantly in areas with rocky bottoms or other areas where they can hide. They grow slowly, not attaining a marketable size of over 3" until two years of age (Kimsey et al. 1982). Nonetheless, they are the dominant crayfish harvested from the Delta with an annual landing of about 250 tons in the early 1980s.

Red swamp crayfish (*Procambarus clarki*) are the principal cultivated crayfish in their native Louisiana and in other states. Their value as a food item is largely due to their very rapid growth; they can reach marketable size of 3" in three months. They were first introduced into California at Los Angeles in 1924 and have now spread through most of the state (Kimsey et al. 1982). Red swamp crayfish prefer warmer waters than *Pacifasticus*, and are frequently found in rice fields and in sloughs with abundant emergent vegetation. They dig a 2" diameter burrow as deep as 40" into dikes and streamsides. By plugging the burrow with mud they are able to survive complete dewatering of the stream or rice field. They can also survive in stagnant waters by using atmospheric oxygen and can tolerate salinities as high as 30 ‰. Another burrowing crayfish, *Orconectes virilis*, escaped into California waterways in 1940 from holding ponds at Chico State College. Both species burrow and eat young rice shoots and are considered pests by rice farmers.

The distribution and abundance of the various crayfish, and the effects of environmental factors, have not been investigated.

4.7 Trends in Fish Abundance

The fishes of the Estuary can be grouped in several ways. The only completely estuarine species of fish is the Delta smelt (*Hypomesus transpacificus*), although the similar longfin smelt (*Spirinchus thaleichthys*) occurs very rarely outside the Golden Gate; all other species maintain at least part of their population outside of the estuary. Sacramento splittail has become a *de facto* estuarine species because suitable habitat for it is no longer present in the Central Valley. The absence of many estuarine species reflects the geologic youth of the estuary. Non-estuarine species consist of freshwater fishes with most of the populations occurring east of Carquinez Straits, marine species which are seldom found east of Carquinez Straits, and anadromous species which spawn in upstream river channels and which predictably migrate downstream through the Estuary as juveniles and upstream as spawning adults.

Freshwater species include both native and introduced species. Native species had been isolated from other regions by geological action and glacial movements; isolation and a strongly seasonal climate promoted the development of a highly endemic fauna with two characteristic types of fish: minnows which spawn only in appropriate years and spiny-rayed fishes which spawn each year and show high degrees of parental care. Most native fishes are minnows (Cyprinidae and one catostomid) which grow to very large size: Sacramento splittail (*Pogonichthys macrolepidotus*), Sacramento squawfish (*Ptychocheilus grandis*), hitch (*Lavinia exilicauda*), Sacramento blackfish (*Orthodon microlepidotus*), hardhead (*Mylopharodon conocephalus*), thicktail chub (*Gila crassicauda*), and Sacramento sucker (*Catostomus occidentalis*). These fish are able to defer spawning in years when little suitable spawning substrate is available and to redirect energy from reproduction into somatic growth. These species are broadcast spawners with little care given to the young aside from the selection of spawning site. Fecundity in these species is directly proportional to size. By deferring reproduction these fish increase their reproductive capacity for later years. Intensive care of young and generally wide environmental tolerances characterize prickly sculpin (*Cottus asper*) and Sacramento perch (*Archoplites interruptus*), in which the male guards a nest (Mathews 1965; Kresja 1967), and the live-bearing tule perch (*Hysterothorax traski*). Sacramento perch are now extremely rare in their native range but survive as populations established in isolated, environmentally harsh habitats elsewhere. Both prickly sculpin and tule perch still live in all habitats of the Central Valley from trout streams to Suisun Bay. Native fishes in the Delta are predominantly restricted to areas dominated by Sacramento River waters (Sazaki 1975).

Many freshwater species were introduced into California from eastern North America by immigrants who wished to fish for the fishes they had known back home. These introductions were greatly facilitated by the completion of the transcontinental railway. Many eastern genera have become dominant members of the local ichthyofauna, including many centrarchids (*Lepomis*, *Pomoxis*, and *Micropterus*) and ictalurids (*Ameiurus*). Common carp (*Cyprinus carpio*) were introduced during early efforts of the Department of the Interior to improve inland fisheries. More recent efforts to manage aquatic resources by changing

Species composition have focussed on intentionally altering trophic interactions in communities. Threadfin shad (*Dorosoma petenense*) were imported as a forage fish for micropterus in upstream reservoirs; inland silversides (*Menidia beryllina*) were brought in as a predator on abundant gnat populations in Clear Lake. Both species are now well established in the estuary. Most introduced freshwater species are more abundant in channels dominated by waters of the San Joaquin River.

Marine species can primarily be divided into those which are seasonally present and those which maintain at least part of their population in San Francisco Bay year-round. Probably because of their large populations in the ocean, seasonal species comprise many of the most abundant fishes to be found in the bay. Northern anchovy (*Engraulis mordax*) is often two to ten times as abundant as other fishes in the Bay; Pacific herring (*Clupea harengus*) is often the second most abundant species, but catches of adults in both species are seasonal and regularly fall to less than a hundredth of their peaks. Northern anchovy regularly enter the bay as adults and stay for as many as nine months. Eggs and larvae of northern anchovy are also caught indicating that all life stages can use the estuary, but none stays year-round. Pacific herring enter the bay for spawning and adults are present in abundance for only a few months. Other seasonal species spawn offshore and rely on density-driven bottom currents, augmented by tidal forces, to carry their offspring into the bay. Starry flounder (*Platichthys stellatus*) and English sole (*Parophrys vetulus*) best exemplify this pattern of use of the bay. Other seasonal species can be less clear in their patterns of using the bay. White croaker (*Genyonemus lineatus*) most often spawn in the Gulf of the Farallones, and many young enter the Bay (probably assisted by tidal or bottom currents). However, in some years adult white croaker occur abundantly in the Bay and may spawn in the shallows. Species that rely on bottom currents for transport should be adversely affected by low river outflow because low outflow cannot provide the density stratification necessary to propel ocean water into the bay.

Resident marine species often fluctuate in their abundance in the Bay from year to year, apparently in response to the distribution of marine waters. Most of these species are benthic. Shiner perch (*Cymatogaster aggregata*), bay gobies (*Lepidogobius lepidus*), and taghorn sculpins (*Leptocottus armatus*) are the three most abundant resident marine species from otter trawl catches. Several other species in the same three families make up the majority of other species in this group. Like the native freshwater species, these species show high levels of parental care (either live-bearing or well protected nest sites) combined with wide environmental tolerances. This category also includes recent importations from the estuaries of Asia that were probably introduced by the discharge of ballast water from international freighters: yellowfin gobies (*Acanthogobius flavimanus*) and chameleon gobies (*Tridentiger trionocephalus*). The survival of a transoceanic passage in ballast water probably selected the hardiest and most human-tolerant species from Asian seaports. Resident marine species generally show little response to flow and include several of the least surviving fish populations in San Francisco Bay.

Anadromous species use the Sacramento-San Joaquin estuary only as a temporary passage but they have tremendous economic and aesthetic value for many people of the Bay and Delta. Native anadromous species include chinook salmon, steelhead trout, and both green and white sturgeon. Despite the extreme seasonality of outflow, the Sacramento-San Joaquin Rivers supported salmon runs in every month of the year and early settlers's accounts include descriptions of staggering quantities of salmon in the rivers. The eminent ichthyologist David Starr Jordan was one of the first scientists to enter the Central Valley. His account includes a description of salmon so densely packed that one could almost walk across the river on their backs. Other observers recorded that the abundance of spawning salmon was sufficient to deter horses from crossing streams near the McCloud River.

Early introductions from the east coast of North America included the anadromous American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*). Populations of these species exploded from their initial plantings and rapidly spread to nearby rivers. Conditions in the rivers at the time of completion of the transcontinental railway probably favored striped bass and American shad reproduction, because their semi-buoyant eggs would not be smothered by silt from gold mining operations. Both species supported commercial fisheries in the bay about six years after their introductions. Most other early fish introductions were of nest building fishes in which the adults select the spawning site and, to varying degrees, keep the eggs clean.

Anadromous species are sensitive to a wide variety of environmental changes including upstream alterations of spawning habitat, altered access to spawning habitat, changes in flow patterns that interfere with migration, and conditions in the estuary that reduce its value as a nursery site for outmigrating young.

4.7.1 Methods

In examining the three main data sets for fishes of the Sacramento-San Joaquin estuary, we have attempted to compare fish which are similar in their habits but different in their distribution or patterns of occurrence in the estuary. For each kind we examine the distribution and trends, if any, for each species. Less abundant species exhibiting similar patterns are referred to where appropriate. Three data sets were used for most of these analyses: the CDF&G Midwater Trawl Survey, the CDF&G Bay Study, and the University of California and Department of Water Resources study of the fishes of Suisun Marsh.

Each sampling program and each type of equipment has its own set of biases in what it catches efficiently. All of these data sets are biased against the capture of species that prefer to live in or around structures such as pilings or that live in rocky habitats. Many sculpins, gobies and surfperches occur abundantly in such unsampled habitat. Both the CDF&G Bay Study and the UCD Suisun Marsh study use seines to sample fishes that occur in shallow, edge habitats but those data are not included here. A number of species that occur regularly in seine hauls are rare in trawl catches including, in Suisun Marsh, inland silversides and chinook salmon smolts. Otter trawls have a characteristic bias toward catching more bottom

oriented species but in shallow habitats will catch a higher proportion of surface-oriented species than in deeper habitats. Midwater trawls sample more of the water column, particularly because CDF&G hauls are brought upward during the course of the trawl; thus, in shallow habitats they will be sampling at the surface a greater proportion of the time than in deep habitats and the catch will have proportionately greater catches of surface-oriented fish. All biases should be consistent for all years and will not affect the analysis of trends at a given station through time. Fish that prefer to live in habitats that are poorly sampled or that have shifted their distribution through time are more difficult to assess.

The CDF&G Bay Study uses both midwater and otter trawls and samples throughout the bay complex in all months of the year. A full description of the sampling regime is available in Armor and Herrgesell (1985). Stations were excluded that were not sampled in all years. Use of the same sampling sites in all years allows us to avoid constructing indices of abundance, instead relying on simple catch per unit effort. No sampling was performed in December of 1980 and in most of our analyses we have excluded data from all December collections in order to eliminate differences in catch due to seasonality so that trends across years could be identified. The 35 stations used included:

- ten stations in South Bay,
- six stations in Central Bay,
- eight stations in San Pablo Bay,
- eleven stations in or adjacent to Suisun Bay.

Depth was measured at each sampling location on each date, but we have used the average depth to characterize the site. Salinity and temperature data are available for surface and bottom waters. This dataset spans the 9 years from January 1980 to December 1988.

Comparisons of changes in spatial distribution reveal other ways that species have responded to reduced flow regimes of the period from 1985-1988 in comparison to the variable flows from 1980-1984. Graphs of the catch of each species of interest at each of the stations that were sampled in all years of the Bay Study are used to show these changes in distribution.

Catches within the Fall Midwater trawl program are predominantly from September, October, November, and December for most of the years from 1967 to 1988. Description of the sampling regime is available in Stevens and Miller (1983). We primarily examined data from the month of September. The abundances from this month reflect the results of the preceding water year, data from other months showed effects of the onset of the next rainy season in the abundance and distribution of several species. In addition, the data from September gave a high number of stations that were sampled in each of 19 years. Other months were more haphazardly sampled, presumably because of foul weather and shorter days in the later months. Restricting the analysis to September also allows separation of the effects of one water year from the next; cursory examination of the data shows that years of high variability in outflow in October are years of large differences between the catches of September and those of October. Samples from stations from the upper reaches of the San Joaquin River were particularly irregular in later months. Unless stated otherwise, data

presented here from the Fall Midwater Trawl (MWT) survey are for September for the stations:

MWT323 and 338 in upper San Pablo Bay,
MWT405, 412, 414, 416, and 418 in Suisun Bay,
MWT604 in Grizzly Bay,
MWT503, 507, and, 515 in Honker Bay and upper Suisun Bay,
MWT606 and 608 in Montezuma Slough,
MWT710, 703, 705, 707, and 709 in the Sacramento River, and
MWT802, 804, 806, 810, 812, 814, 904, 906, 908, and 910 in the San Joaquin River.

Each of these 28 stations was sampled in all years from 1967 to 1988 except 1974, 1976, and 1979. Data from other stations are used to compare with other data sets in less sampled areas. A single depth measurement (m) was used to characterize each study site for the length of the study, although factors such as tide and outflow resulted in depths at each site varying as much as one meter among sampling times. Salinity and temperature are generally available only for the surface water.

The UC Davis/DWR sampling is confined to Suisun Marsh, at the uppermost end of the bay complex. Sampling has been monthly from January of 1979 to May 1990 at 17 stations in the shallow sloughs of the marsh. A full description of the sampling regime is available in Herbold (1988) and Moyle et al. (1985). Salinity and temperature data were taken at each site; stations are mostly less than 2 m deep and no evidence of stratification has been found.

Historical data sets used for comparison were those of Pearson (1989) for fishes of the South Bay and Aplin (1967) for fishes of South and Central Bay. Sazaki (1975) was consulted for evidence of distribution of fishes in the Delta.

Abundance data for species of interest were summarized for each month at each station and embayment by (1) number of individuals per trawl, (2) presence or absence of the species of interest, (3) number of individuals caught per month, and (4) total catch of the species per year. For species in which different stages are ecologically distinct we have separated the analysis for young, juveniles, or adults as necessary. Data on lengths were only available for the Bay Study and the last three years of the Fall Midwater trawl survey.

Data on flows are derived from the DAYFLOW data set provided by the Department of Water Resources: annual and monthly averages were calculated from the daily flows.

Descriptions of the status and trends of more intensively studied species are based on published studies and personal communications with the principal investigators; these species are chinook salmon, striped bass, white sturgeon, and Pacific herring. Accounts of status and trends for less studied species are largely based on the data sets described above. The less studied species are grouped by similarities of feeding modes. Northern anchovy, Pacific herring, delta smelt, longfin smelt, American shad, and threadfin shad are all planktivores which strain or pick zooplankton from open water. Starry flounder and English sole are flatfishes which feed on benthic animals. Surfperches pick small animals from the surfaces

of aquatic plants and other structures, as well as from the bottom. White croakers eat larger animals, including fish, from the bottom or midwater regions.

4.7.2 Chinook salmon

Chinook salmon grow to almost 1.5 m, larger than any other species of salmon (*Oncorhynchus tshawytscha*; Figure 30). They make up the largest commercial finfish fishery near San Francisco and also support a very large sport fishery in the ocean. In the Bay, which is open only to sport fishing, the fishery is much smaller. Marked fingerlings from the Sacramento-San Joaquin Estuary have been caught as adults all the way up the west coast to Vancouver Island. The Central Valley supports the largest population of salmon in the state, but the population has suffered very large declines of the wild stocks. The population is now maintained to a large extent by hatchery operations.

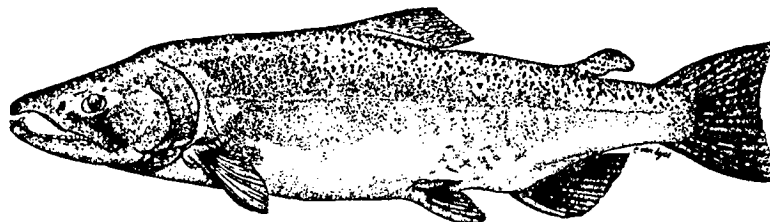


Figure 30 Chinook salmon, adults typically 75 cm (from Moyle 1976)

Salmon abundance in the Sacramento-San Joaquin Estuary prompted massive fishing efforts and the opening of the world's first salmon cannery in 1864 (Skinner 1962). The only quantitative statement on the early abundance of chinook salmon are the records of this company, which show export of 48 tons in the first two years of operation. More canneries opened and more commercial fishing led to a mean annual catch of more than 3,000 tons until commercial salmon canning was banned in the Bay in 1919 (Skinner 1962). Except for a brief resurgence in the 1940s, the commercial catch in the Estuary remained at low levels from 1920 to its end in 1957 (Skinner 1962).

Chinook salmon originally spawned throughout the tributaries or upper reaches of the Sacramento and San Joaquin River Basins. About half of the potential spawning habitat in the Sacramento River Basin was blocked by construction of Shasta Dam. Other dams were constructed on the American and Feather Rivers. Hatcheries were constructed to attempt to offset the effects on salmon populations of these blockages. In the San Joaquin River Basin, Friant Dam blocked access to much of the mainstem San Joaquin River and totally eliminated salmon from the mainstem and upper tributaries. Dams also blocked the Merced, Tuolumne, and Stanislaus Rivers, the major downstream tributaries. A small hatchery on the Merced is the only attempted mitigation for these upstream habitat losses. As a consequence of these actions in both the Sacramento and San Joaquin Basins, some runs have been almost totally extirpated, the run balance has shifted to strongly favor fall run fish, and much of that run now consists of fishes raised to the fingerling stage in hatcheries.

Individual adult chinook salmon spend very brief periods in the Sacramento-San Joaquin Estuary during their upmigrations. Outmigrations of smolts are spread out over a longer period because they spend daylight hours along the edges of streams and usually slowly migrate downstream at night when outflow is low and the water is clear. Under higher flow and turbidities, daytime migrations may take place as well. Within the Delta, higher turbidities probably lead to little difference in downstream migration rates between day and night. The species is divided into four distinct runs which travel through the estuary at different times so that it is possible to find adults and juveniles passing through the estuary in any month of the year when temperatures permit (Figure 31). Adult salmon migrate through the estuary very rapidly, usually in a few days, with individuals of the endangered winter run passing through most quickly (Hallock and Fisher 1985). The only study of adult migration through the estuary to tag individual fish was conducted 25 years ago (Hallock et al. 1970). Opening of the cross-Delta channel brings Sacramento River water into the central Delta and causes delays of adult salmon migration (Hallock et al. 1970). Such delays can lead to failure of female fish to find appropriate spawning sites before having to release their eggs. High temperatures, low oxygen concentrations, and high biochemical oxygen demand are interrelated variables which have been shown to block migration of adult salmon of the San Joaquin Basin. Increased sewage treatment (particularly in Stockton), operation of New Melones Dam to provide greater flows, improved water quality, and a temporary barrier at the head of Old River have improved spawning success of Stanislaus, Merced, and Tuolumne river populations (USFWS 1987). The shortage of water in all three drainages during the 1985-1991 drought resulted in extremely low returns to the San Joaquin drainage (CDF&G unpublished data). High diversion rates relative to flow lead to decreased ability of the runs to find their natal streams (USFWS 1987).

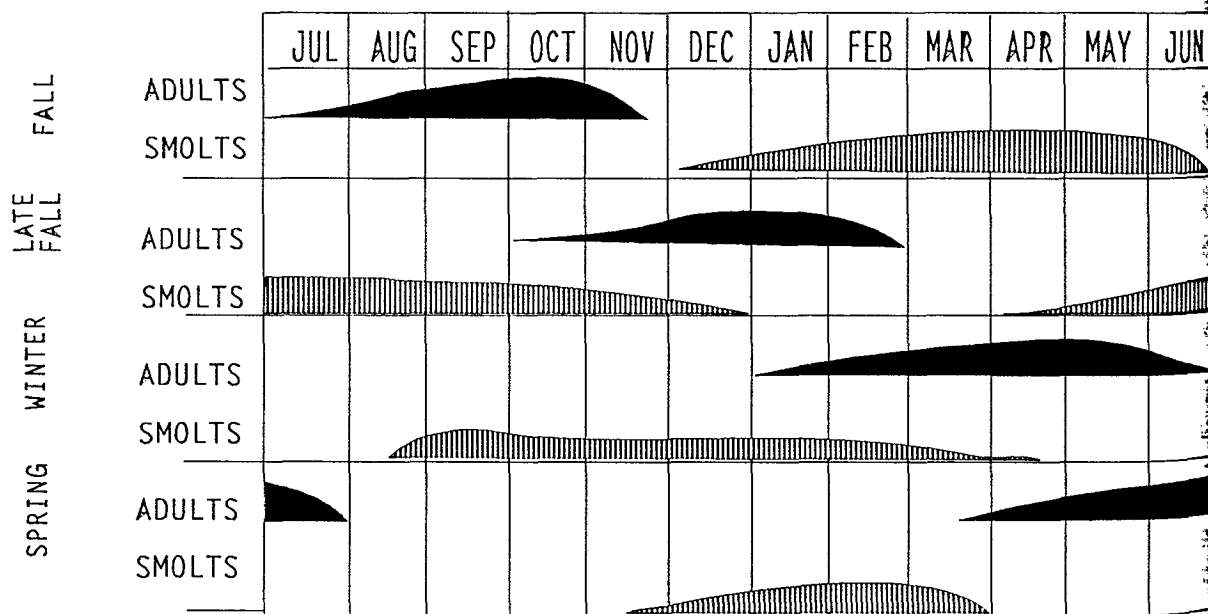


Figure 31. Periods of migration for the four runs of chinook salmon through the Sacramento-San Joaquin River system. (modified from USFWS 1987)

Passage through the Delta is a critical step in chinook salmon smolt survival (USFWS 1987; Herrgesell 1990). Tagged smolt releases further downstream in San Francisco Bay show greater survival and rates of return to natal streams than releases in the Delta or downstream areas (USFWS 1987). The large number of hatchery raised fish makes it difficult to discern the factors affecting the production by wild populations. After hatching, wild smolts remain in fresh water for spend extremely variable periods before beginning their downstream migration. Although the potential exists for smolts to migrate through the Delta in every month of the year, smolts are rarely observed from July through September due to high temperatures (USFWS 1987). Smolt migration through the Delta has been estimated at 10 to 20 miles per day (USFWS 1987). Migration rate through the Bay and Sacramento River side of the Delta is slower than in the upper reaches of the rivers and does not seem greatly affected by flow rates as it is in more upstream reaches (USFWS 1987). Migration of smolts through the San Joaquin portion of the Delta, however, does seem to be related to flow. During their passage through the Delta, fall run smolts are particularly liable to suffer increased mortality if they enter the Central Delta (USFWS 1987). Passage through the Central Delta is detrimental to smolts because of warmer temperatures, increased predation rates, longer migration routes, areas of reverse flow in river channels, and entrainment by agricultural and export pumps (Herrgesell 1990).

High correlations have been found between flow (as estimated at Rio Vista) and smolt abundance and survival (USFWS 1987; Figure 32) and between flow and survival (FWS/DWR 1989). The correlation appears related to the interrelationships between flow, water temperature, and the percent of flow diverted to the central Delta. Salmon smolt survival decreases as water temperature and percent of flow diverted into the central Delta increase.

To separate the effects of several factors affecting smolt survival on their passage through the Estuary, the Interagency Ecological Study Program performed an experimental series of releases of hatchery fish in 1989. Fish were released:

1. at various sites to examine the effects of different migration routes.
2. at the same sites in different months with the same outflow to investigate the effects of temperature.

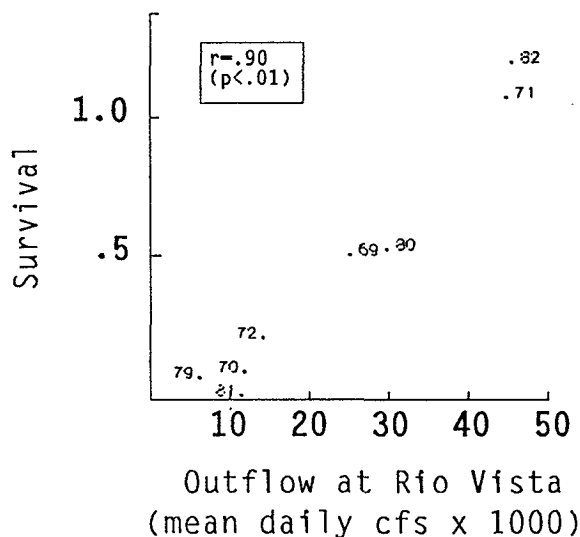


Figure 32 Relationship of smolt survival to mean daily outflow at Rio Vista during outmigration. Label numbers indicate year of outmigration (modified from USFWS 1987)

3. above and below Walnut Grove when diversion gates of the Cross-Delta Channel were open and when they were closed in order to determine degree of impact of the cross channel operations on outmigration.

Results from these studies indicated that:

1. shorter migration routes which avoid the Central Delta appear to be beneficial for smolt outmigration.
2. smolt survival increased at lower temperatures
3. survival of smolts released above the Delta Cross Channel was lower when the gates were open.

Within San Francisco Bay, a concern of how conditions may affect salmon numbers is through the dumping of dredge spoils at Alcatraz Island, which may reduce entry of adults into the estuary (Quinn 1990).

Because habitat loss has more greatly reduced the abundance of other runs, because operation of Shasta Dam favors spawning of fall run, and because hatchery production is mainly of fall run fish, the fall run now accounts for 90% or more of the 200,000 to 1,000,000 salmon of the ocean fishery (USFWS 1987). The amount of disruption of the fall run has also been less in the Sacramento River than in the San Joaquin River so that recently, the San Joaquin River accounts for 1 to 22 percent of the fall run spawners (Herrgesell 1990).

The most reduced run is the winter run which was listed as endangered by the California fish and game commission and as threatened by the National Marine Fisheries Service in 1990 after its spawning run size was estimated as slightly more than 500 fish. Listing as endangered had been proposed in 1985 because the species had declined from recent runs of 20,000 - 35,000 (1970-1978 runs averaged over 30,000) to runs of 2,000 - 3,000 fish. (National Marine Fisheries Service 1987; Williams and Williams 1991; Figure 33). The run in 1991 included only 191 spawners. Like the fall run, the winter run spawn primarily in the main stem of the Sacramento River. However, spawning and egg incubation occur in the spring and summer and outmigration not until fall and early winter. Low and fluctuating flows and high water temperature during this time cause extensive mortality. Prior to the construction of Shasta Dam, this run spawned primarily in the cold, spring-fed waters of the McCloud River and a few other tributaries. Shasta blocked access to these spawning grounds but provided sufficient cold water in many years to permit spawning in the reaches immediately below the dam. Construction of Red Bluff Diversion Dam later reduced access to areas below Shasta Dam. These problems of temperature, flow, and access were exacerbated by the drought of 1976-77 and the drought beginning in 1987. The ability of the winter run to recover its former numbers is further reduced because adults return to spawn after only two or three years at sea; therefore adults are smaller than in other runs and have a proportionately lower fecundity (Hallock and Fisher 1985).

Spring run adults enter tributary streams and hold in them through the summer months while their gonads mature (Marcotte 1984). This life history pattern has made them very

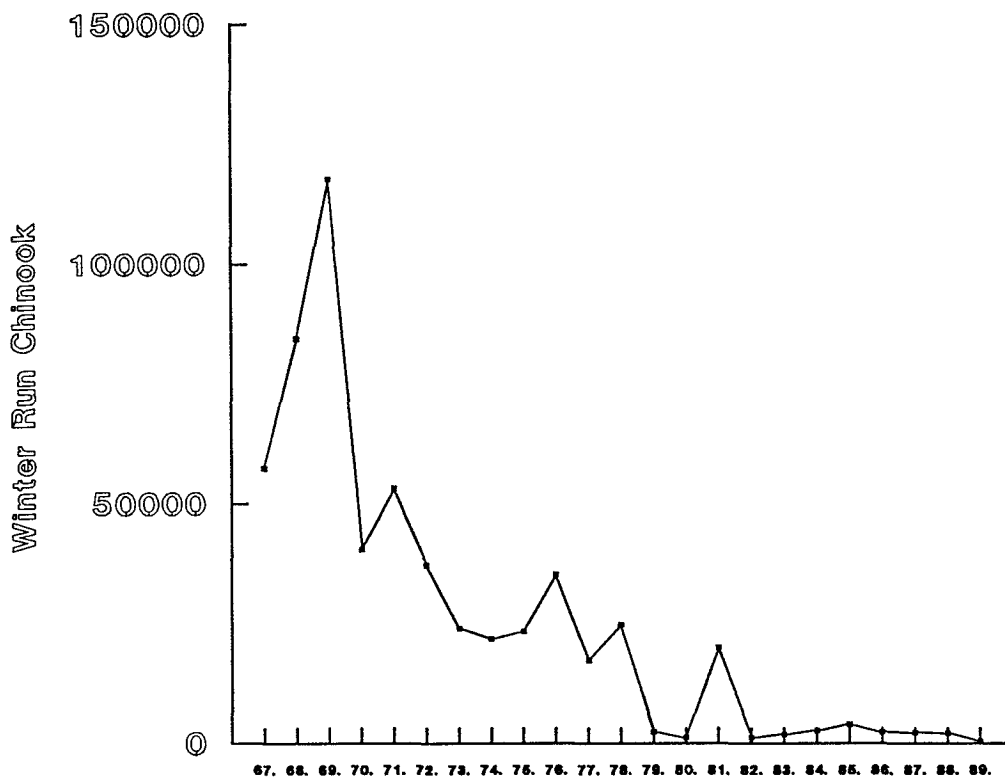


Figure 33 Estimated population of returning winter run chinook salmon in the Sacramento River. Data from Moyle et al. 1989.

sensitive to dams that block their access to holding pools and spawning sites or which reduce summer flows through their holding pools or spawning sites so that temperatures rise to stressful or lethal levels (Moyle et al. 1989). Because of widespread damming of streams and the sensitivity of the spring run to damming, the spring run has declined from being the most widespread and abundant run in the Central Valley to populations of only 3,600 to 7,000 in the years between 1969 and 1980 (Marcotte 1984). However, the spring run which spawns in the upper Sacramento River has been relatively stable at around 15,000 fish, although its genetic integrity is doubtful. Likewise the run on the Feather River is stable at around 2,000 fish, although it is largely supported by hatchery production. Runs of wild fish in Butte, Big Chico, Mill, and Deer Creeks have all declined to less than 1,000 fish total, and are continuing to decline (Campbell and Moyle in press). Construction of Friant Dam provided a well-documented extermination of the spring run in the San Joaquin River (Warner 1991). Similarly, populations were eliminated on other San Joaquin Basin tributaries and a large population was eliminated from the American River Basin. Construction of LaGrange Dam on the Tuolumne River doubtless destroyed a salmon population in that stream but data prior to construction are scant.

4.7.3 Striped bass

The introduction of striped bass (*Morone* [previously *Roccus*] *saxatilis*; Figure 34) in 1879 led to a commercial fishery in the estuary within 10 years (Craig 1928). The spectacular success of this fish is very similar to that of American shad, which were introduced in 1871 and supported a commercial fishery 8 years later (Skinner 1962).

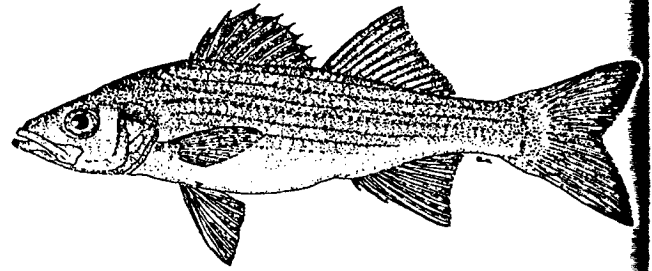


Figure 34 Striped bass, adult maximum length about 120 cm, yearlings about 15 cm . (from Moyle 1976)

Both successes can probably be attributed, in large measure, to the anadromous nature and semi-buoyant, non-adhesive eggs of both species. Being anadromous brought the initially few adults together in a limited area so that the broadcast eggs and sperm would be likely to find each other, while the young were carried downstream and did not have to deal with a river that was naturally very variable in flows and temperatures and which was being massively affected by human actions. The semi-buoyant eggs were not susceptible to suffocation by the tremendous quantities of silt released into the streams by hydraulic mining.

However, the striped bass introduction differs in one major respect from that of American shad. American shad travel widely in oceans and, after their planting in California, they were found to naturally invade many other rivers on the Pacific Coast (Moyle 1976). Striped bass have been captured from central Oregon to southern California, but most of the Estuary's striped bass do not travel more than 40 km from the Golden Gate during their time in the ocean (Chadwick et al. 1977; Stevens et al. 1985).

Striped bass is the principal sport fish caught in San Francisco Bay. In the Delta more angler hours may be spent in pursuit of catfish and other panfish, but the large industry supporting the needs of striped bass enthusiasts make the striped bass more important economically. The subsidiary industries surrounding striped bass fishing (boats, marinas, and paraphernalia) are estimated to bring \$45 million into the local economies (Meyer Resources Inc. 1985). Declines in the fishery since 1970 are estimated to have cost the state more than \$28 million per year (Meyer Resources Inc. 1985).

The tremendous growth of the striped bass population, from two initial plantings of 132 fish in 1879 and 300 fish in 1882, reflects the enormous fecundity of this species (Skinner 1972). Females commonly broadcast from 500,000 to 4.5 million eggs (Hassler 1988) although estimates range from 11,000 (Moyle 1976) to a high of 5.3 million (Hollis 1967; Hardy 1978; Wang 1986). Conditions in San Francisco Bay during the 1880s allowed many eggs to grow to adulthood. By 1889, the striped bass fishery was landing more than 454 tons each year until 1915 (Smith and Kato 1979). Either through overfishing, habitat degradation, or the usual decline in abundance following the successful introduction of a species, the population of striped bass appears to have begun declining in the early years of

the 20th century. Finally, in 1935, commercial fishing for striped bass was banned. Despite the removal of commercial fishing, the striped bass population seems to have continued its decline. Catch per angler per year steadily dropped from more than 20 fish in the 1930s, to more than 10 in the 1940s, and finally less than 10 through the 1950s (Skinner 1962). To some extent the decline was attributed to degradation of the Bay as fish habitat. Former popular fishing grounds in South Bay and in the Napa River were abandoned both by striped bass and anglers due to pollution and habitat loss (Skinner 1962). Identification of the declining trend in catch per angler (Skinner 1955, cited in Skinner 1962) led to tighter restrictions and catch limits so that later catch per angler figures are not comparable. However, the fishery continued to attract and satisfy a large number of Bay area anglers until the late 1970s (Meyer Resources Inc. 1985). Given that the population of anglers was probably increasing in proportion to the growth of the human population overall, it is impossible to know if catch per angler reflects the size of the striped bass population.

Scientific monitoring of the striped bass population began in 1959, and in the early years of study the population showed greater production of young in most years than it has shown

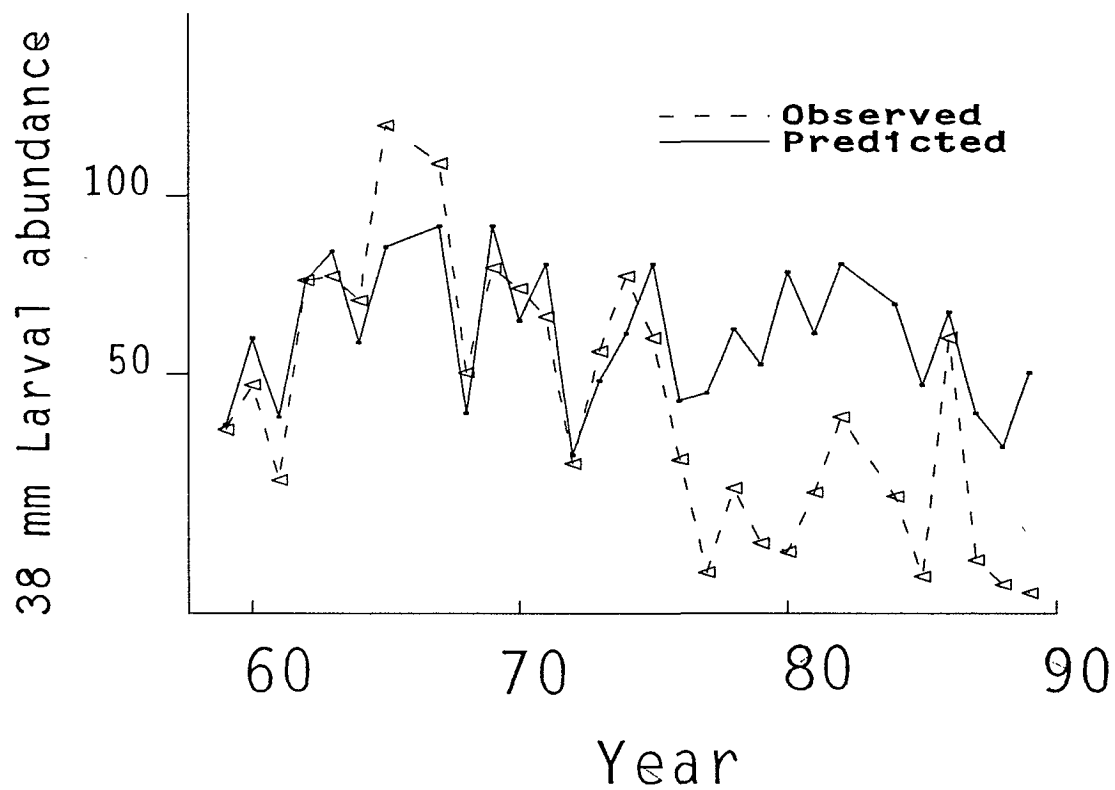


Figure 35. Comparison of actual striped bass index values with those predicted from a regression equation based on outflow and diversion rates.

most recent years. Examination of the first 15 years of the study showed a high correlation of 38 mm bass abundance with Delta outflow (Turner and Chadwick 1972).

A regression equation, based on Delta outflows and diversion rates, very effectively modeled striped bass abundance.

The mechanism by which outflow controlled larval recruitment was unclear. High outflows were thought to provide the following benefits (Turner and Chadwick 1972; Stevens 1977b):

1. larger nursery areas so that intraspecific competition would be minimized;
2. more shallow habitats producing more primary productivity leading to greater food abundance for larval bass;
3. more water to dilute pollutants;
4. greater turbidity and less dense concentrations of young to reduce predation; and
5. smaller danger of entrainment into diversions from the Delta.

Unfortunately, for most of the following years, the model seriously overestimated the abundance of young bass (Figure 35). The failure of the model to accurately predict striped bass production coincides with a severe decline in striped bass abundance. Population estimates for the total population of adults in the estuary were between 1,480,000 to 1,880,000 for the years prior to 1976; from 1977 onward the population ranged from 520,000 to 1,160,000 (CDFG unpublished data).

A variety of causes for the decline have been put forward with varying degrees of supporting evidence: toxic effects, larval starvation, increased entrainment, and declining egg abundance. Among people who fish for striped bass a popular explanation was based on the presence of ulcers on the left side of many adult striped bass. The possibility that a new disease was decimating the population was discussed in the popular press. However, the tapeworm (*Lacistorhynchus tenuis*) responsible for the ulcers appears to be neither virulent nor abundant enough to produce such a massive change in the population. The following summary of factors sufficiently widespread to be responsible is based largely on the discussion in Stevens et al. (1985) and Herrgesell (1990).

Toxics. Toxic contamination of Sacramento River water flowing into the Delta increased several-fold during the mid-1970s as rice farmers switched to growing short stem rice which entailed higher applications of pesticides (Foe 1989). Concentrations high enough to kill fish were found during monitoring surveys in several sloughs near rice fields in the Sacramento Valley. Concentrations calculated to have occurred in the mainstem of the Sacramento River during the 1977 drought may have posed a serious threat to striped bass larvae (C. Foe, pers. comm.). Studies of the toxicity to striped bass larvae and to *N. mercedis* of drain water entering the Sacramento River have been undertaken by the California Regional Water Quality Control Board - Central Valley Region (Foe 1989) and the Department of Fish and Game (Finlayson et al. 1991). Both studies demonstrated acute toxicity of the water to *N. mercedis*. Bioassays using striped bass larvae showed toxicity when conducted by the University of California, Davis for the Regional Water Quality Control Board, but tests by

CDF&G did not. Differences in results may be due to different salinities at which the tests were run (Foe, pers. comm.). Release of contaminated water from rice fields coincides closely both in time and space with the spawning of striped bass (Foe 1989). Calculations of the likely concentrations of toxics in the river in each year since 1977, when the rice growers began much greater use of toxics, accounts for 42% of the difference between expected and observed abundance of striped bass young in the Delta (Foe 1989).

Other evidence of the influence of toxic contamination has come from histological work performed by D. Hinton and W. Bennett of the University of California, Davis. Liver sections from larvae from the Sacramento River show much higher incidence of malformation than larvae from elsewhere. No quantitative estimates of mortality due to toxic compounds are available. Although the concentrations of toxics in the flesh of adult striped bass is monitored now, there is no comparable data from before the decline that would allow estimation of changes in the toxic load carried by striped bass.

Larval starvation. The composition and abundance of food for larval bass has changed drastically since 1979. Introduced copepods, principally *Sinocalanus doerri*, have partially replaced the formerly abundant copepod *Eurytemora affinis* (CDF&G 1987b). In feeding experiments striped bass larvae, when they first start to feed are much more adept at capturing the native *E. affinis* and *Cyclops spp.* than they are at capturing the introduced *S. doerri* and slightly less adept at catching

Pseudodiaptomus forbesi, another exotic species (Herrgesell 1990; Meng and Orsi 1991). The reason for the failure of larvae to feed effectively on the currently abundant *Sinocalanus* seems to be that the introduced species has more effective escape responses. However, histological analysis of striped bass larvae collected from the wild have failed to show any signs of starvation (W. Bennett UCD, pers.comm).

Laboratory feeding experiments with striped bass have established a surprisingly tight relationship between food density and larval survival (Figure 36). Estimates of larval mortality rates and food abundance in the Sacramento-San Joaquin estuary were compared to those expected from these laboratory studies. Although food rates are lower than in most of the laboratory studies, mortality rates are substantially higher than expected (Figure 36). Thus, larval bass in the estuary are dying more rapidly than larval bass at similar food

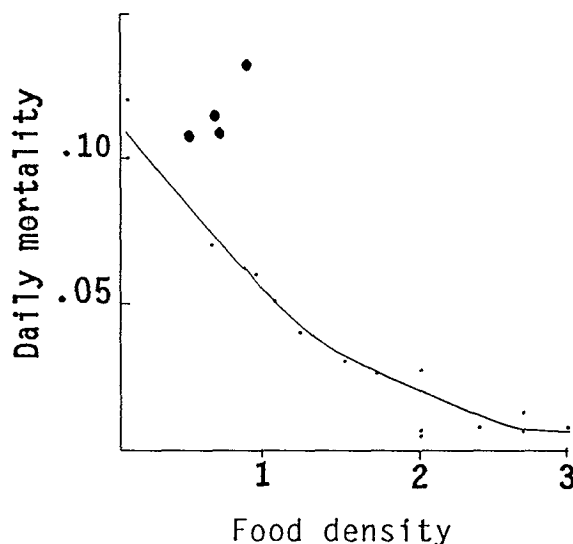


Figure 36 Relationship of food abundance and mortality in laboratory conditions (line and small dots) to conditions in Delta (large dots). Based on Herrgesell 1990.

densities when held in the laboratory (Herrgesell 1990). The only factor expected to kill striped bass in laboratory feeding tests is starvation; if starvation happens in the field, however, it is likely that slower growing or unhealthy fish would suffer increased mortality from other sources. Food densities are much lower than any feedings under laboratory conditions and growth rates are generally half of those observed under any laboratory food densities except complete starvation (Table 2). Food densities in the field are probably much more patchy than under laboratory conditions so the averages reported for the field may mask the presence of dense concentrations in small areas. In short, starvation may be a reasonable expectation for young striped bass, but they show no evidence of it either in their degree of stomach fullness or in histological comparisons with fish that are known to be starved. Extensive studies of striped bass in eastern North America indicate that they have an unusual resistance to starvation and rarely do so in the wild, although fast growing larvae are more likely to reach maturity (J. Cowen, pers. comm). Slower growing larvae are presumably more vulnerable to predation, a phenomenon largely uninvestigated in the Estuary. The decrease in food abundance and the abundance of less easily captured prey species apparently has little to do with the striped bass decline but may make more difficult the recovery of the population.

Table 2. Growth rates of striped bass from various laboratory measurements compared to estimates from field measures in the Sacramento-San Joaquin Estuary. Measurements from Herrgesell 1990 are field estimates. (modified from Herrgesell 1990).

Source	Food density	Growth (mm/d)
FIELD		
Herrgesell 1990	4	.16
	5	.16
	6	.19
	7	.22
LABORATORY		
Daniel 1976	0.0	.036
Daniel 1976	30.0	.33
Chesney 1989	50.0	.30
	100.0	.33
	100.0	.36
Houde and Lubbers 1986	100.0	.22
Chesney 1989	250.0	.40
Houde and Lubbers 1986	500.0	.36

The most recently introduced clam, *Potamocorbula amurensis*, has developed large populations in Suisun Bay, which is a major nursery area for larval striped bass. Filtration by this clam is presumed to be responsible for removal of phytoplankton and consequent failure of zooplankton populations to attain their normal densities. Because the clam was not present in the Bay until long after the population of striped bass had declined it is not possible for it to have been responsible for the decline. If it persists at its present high densities, however, it is possible that it will make restoration of the striped bass population much more difficult.

Hydrology. The decline in larval abundance, and the failure of the earlier regression model to accurately predict larval abundance, was most pronounced in the Delta (Chadwick et al. 1977). The only year since 1976 when predicted larval abundance based on outflow equalled actual larval abundance was in 1986 when flows through the Delta were augmented throughout the spring as a result of record rainfall in February. In Suisun Bay there was an abrupt decline in larval abundance during the 1976-77 drought. In the Delta the decline seems to have begun in 1971-1972 and to have been more gradual. In Suisun Bay, larval abundance has occasionally returned to former levels, and both regions showed high abundances in 1986. However, since the start of a long drought in 1987, larval abundances have declined in both areas so that the 1990 overall index was the lowest ever recorded.

This pattern of more consistent decline in the Delta has focussed attention on mortality causes in the Delta. Movement of eggs and larvae into the Central Delta where they are subject to greater mortality due to entrainment by various diversions is the most obvious control on larval mortality in the Delta. Additionally, 1977 was a year of much higher larval survival than expected for the low level of outflow which is only easily explained by reference to the restricted amount of water diversions by SWP and CVP that year (Herrgesell 1990). The decline in young bass abundance is consistent with a simultaneous decline in egg production by the depleted adult population

Testing of a regression model of young bass survival (rather than abundance) against outflow and diversions not only accounts for the anomalous higher abundance of 1977, but provides a reasonably tight explanation for the decline in young bass abundance since 1977. Inserting a lag term of 5-8 years to allow the young bass to grow to maturity also accurately accounts for the observed drop in the adult stock and its egg production in 1977 (Herrgesell 1990). These adults were the young fish produced from 1969-1972 when the State Water Project began diverting water from the Delta and the Central Valley Project increased its diversions.

The current year-round diversion of most San Joaquin River water toward the export pumps has greatly reduced recruitment from adults spawning in the San Joaquin River in and above the south Delta. Unfortunately, there is no estimate of production from the San Joaquin River prior to the decline, so it is impossible to determine how much production has been lost there. In 1986 the most intensive storm in California records produced an extremely large outflow volume and, for much of the spring, outflow greatly outweighed exports. This was the only year since 1977 when abundance of 38-mm larvae matched the prediction of the outflow-alone model. It has been argued that this was largely due to successful reproduction in the San Joaquin River. The predicted stronger year class of spawners resulting from the higher striped bass index of 1986 has failed to materialize.

Changes in egg production. A smaller adult population must produce fewer eggs, and it has been argued that the decline in recruitment due to entrainment by water project operations may have produced a subsequent adult population size that does not produce enough eggs to maintain the population (Herrgesell 1990). Estimates of egg abundance are far below half of what they were prior to the decline (Figure 37). The lower egg production figures show a five to eight year lag with the estimated impacts of water diversions, due to the bulk of egg production coming from 5 to 8 year old fish. This explanation is supported most strongly by the apparent consistency between pre- and post decline measures of larval survival between each size class. Correlations between one larval size classes and the next are strong and suggest that the initial abundance of eggs should cascade through the larval stages and control recruitment. Decreased egg production may be simply a necessary consequence of a smaller adult population size. It has been frequently pointed out that the initial planting of striped bass, which grew to immense numbers in only a few years, was less than a thousandth of the estimated adult population today. However, the Delta today may allow a smaller proportion of eggs to hatch, and so egg production now may be

sufficient to maintain the population whereas a much smaller population of colonizers flourished in the 1800s.

Conclusions. Increased loss of eggs and larvae into the hazardous Central Delta is the only well-documented and sufficiently powerful mechanism to explain the continuing destruction of the striped bass fishery. Estimates of effective reduction from entrainment were 73 and 84% in the dry years of 1985 and 1988, respectively (Herrgesell 1990). These estimates contrast strongly with the estimated reduction due to entrainment of only 31% in the wet year of 1986. The difference in losses between wet and dry years reinforces the density-independent mechanism that is keeping populations low. Higher outflows move a higher percentage of eggs and larvae out of reach of entrainment, and higher diversions lead to higher percentages of entrainment of eggs and embryos. The fact that the percentage taken is independent of the number present, coupled with ever smaller numbers of eggs produced, makes the interaction of diversion rate and outflow the only adequate explanation for the decline of the population and its inability to rebound.

Although the data and biological reasoning strongly support hydrologic changes in the Delta as the cause of the striped bass decline, one cannot completely dismiss the importance of other factors. The failure to find a difference in mortality rates for different age classes provides only weak grounds for restricting attention to egg production rates among the competing secondary factors. Statistically, failure to reject the hypothesis of no difference is not the same as saying no difference exists (Steel and Torrie 1960). Failure to discern a significant difference may be attributed to the very small sample size of only five years in the pre- and post decline periods, or to data which are inherently too variable to allow the identification of a small difference in means. Even small differences in mortality rates at early life history stages would be enough to account for a major reduction of the adult population. However, mortality rates from a variety of measures are in general agreement. The association of increased diversions and decline in predicted striped bass production provides the most conservative explanation for the continued low production of striped bass abundance and their lowered egg production.

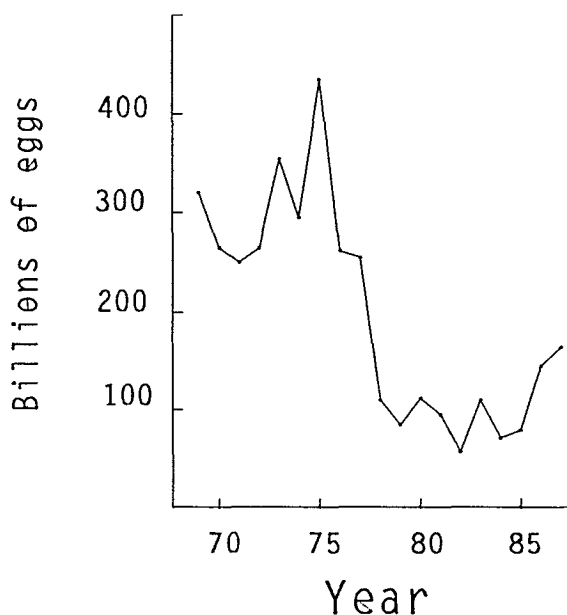


Figure 37. Estimated numbers of eggs produced by adult striped bass population in Delta. (from Herrgesell 1990).

The case for larval starvation is based on lower growth rates and higher mortalities in the estuary than those recorded from laboratory studies. The replacement of native copepods by exotic species, particularly *S. doerri*, is considered to be a possible contributing factor. Although striped bass in the field consume *Sinocalanus*, laboratory studies show that they are much less successful at capturing them than they are with formerly abundant *Eurytemora*. Finally, the introduced clam has substantially reduced zooplankton densities in Suisun Bay, but they did not enter the estuary until ten years after the decline of striped bass. The clam may make recovery of striped bass populations difficult, but it cannot have played any role before 1986. Countering this evidence is the observation that the histological changes accompanying starvation are absent from most larvae collected in the field. In addition there is a lack of persistently lower survival rates during the larval period or the period between 9 and 38 mm.

The possible importance of toxics or food scarcity on striped bass recruitment has been downplayed because there has been no detectable change in age-specific mortality between the pre- and post-decline periods. If larvae are succumbing to pesticides or starving to death one would expect age-specific survivorship to decline through time. With a declining population but no increase in mortality, it is argued that the principal cause of fewer larvae must be fewer eggs. Dumping of toxic waste water into the spawning grounds is also argued to be an adequate way to reduce effective egg production.

The evidence for the importance of toxics rests on the concurrent shift to heavy use of new pesticides at the time of the first drop of striped bass larval abundance from that predicted by outflow. Spawning grounds of striped bass in the Sacramento River are within the areas where rice fields discharge toxic waste water into the river. There is no direct evidence that levels of pesticides in discharged waters from these rice fields have been high enough to kill sufficient larval bass in all years to account for the persistent decline.

Even if toxics or changes in food abundance and catchability are not the primary cause of the decline, they are likely to make recovery efforts more difficult.

4.7.4 Sturgeon

Two species of sturgeon inhabit the Sacramento-San Joaquin estuary: the green sturgeon *Acipenser medirostris*, and the white sturgeon *Acipenser transmontanus* (Figure 38). The green sturgeon is much less abundant, but is often the more



Figure 38 White sturgeon, maximum length today about 3m (from Moyle 1976).

abundant species in smaller Pacific Coast estuaries. The green sturgeon is disdained by many fishermen (Jordan and Everman 1923). California Department of Fish and Game records from tagging studies performed intermittantly since 1954 in the Sacramento-San Joaquin Estuary show that, for legal-sized fish (generally > 102 cm total length), the ratio of green:white sturgeon has varied from 1:39 to 1:164 (Miller 1972a; Kohlhorst, CDFG pers. comm.). Part of the reason for the difference in abundance within the estuary between the two species may be attributed to green sturgeon spending a larger portion of their lives in the ocean (Kohlhorst et al. 1991). The very low abundance of green sturgeon has hindered scientific study of the species, but it is believed to be declining in abundance throughout its range (P. Foley, UC Davis).

White sturgeon appear to be more strictly estuarine in their distribution (Miller 1972a,b) than green sturgeon. Early fishing for sturgeon collected many fish and many large individuals, but the population was rapidly depleted and all fishing was halted in 1917 (Skinner 1962). A sport fishery was reopened in 1954 with a 102-cm minimum size and one fish per day creel limit. The fishery is primarily in San Pablo and Suisun bays and uses shrimp as bait rather than snagging as in earlier years; shrimp used include *Crangon spp.*, *Palaemon macrondactylus*, *Callinassa*, and *Upogebia* (Kohlhorst et al. 1991). As a result of more sophisticated fishing techniques, exploitation rates in the late 1980s were about 40% higher than in the preceding two decades (Figure 39). This may have reduced annual survival rates, abundance, and egg production. Patterns of mortality and abundance suggest that, up to now, population size has been controlled primarily through recruitment (Kohlhorst et al. 1991). Concern about the effect of higher exploitation rates on the population led to increasing the minimum size limit.

Like most of the other harvested fish of the Sacramento-San Joaquin Estuary sturgeon are anadromous, growing and maturing primarily in salt and brackish water and spawning in fresh water. Overfishing in the late 1800s greatly reduced the populations long before any biological research could be done. Research in recent years has attempted to determine the population size, mortality rates, migration patterns, spawning areas, spawning habitat requirements, and factors affecting year-class strength.

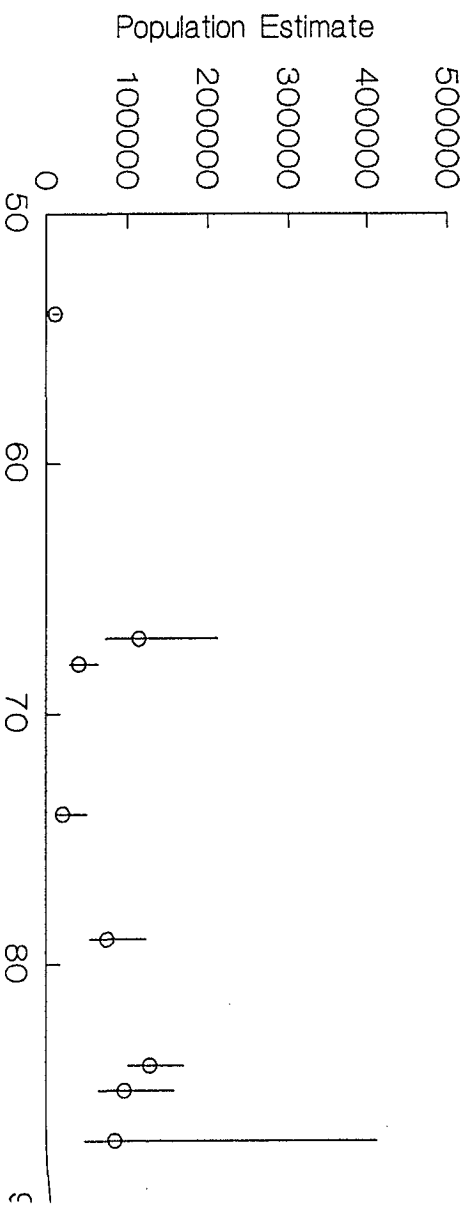
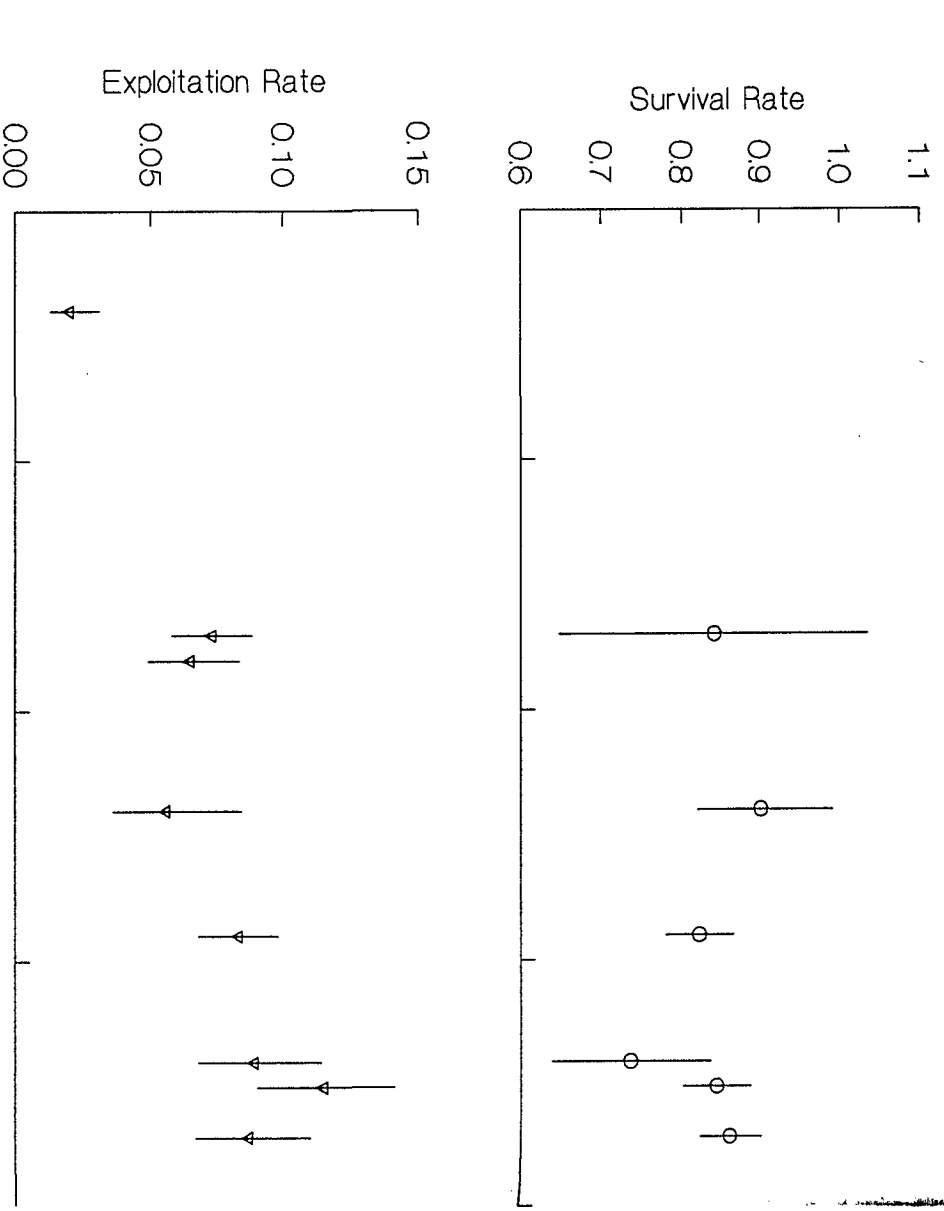


Figure 39 Means and confidence limits of survival, population size, and exploitation rate measured for white sturgeon population in the Estuary (data from Kohlhorst et al. 1991).

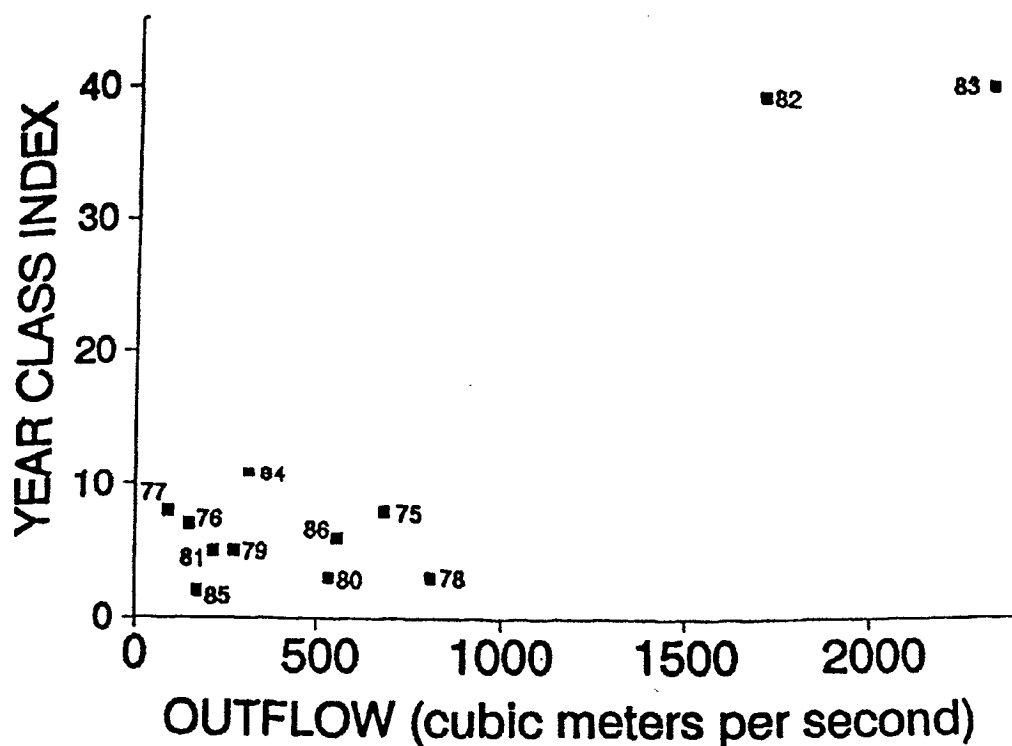


Figure 40 Relationship of white sturgeon production and outflow rates (from Kohlhorst et al. 1991)

Recruitment in white sturgeon appears to be greatest in years of very high outflow (Kohlhorst et al. 1991; Figure 40). Mean daily outflows below $1000 \text{ m}^3\text{s}^{-1}$ during the spawning and nursery period (April-July) are associated with consistently low-year class strength, but outflows over 1500 produce very strong year classes. Data from catches of juvenile sturgeon at the State Water Project fish salvage facilities suggest that mean daily April-May outflows less than $600 \text{ m}^3\text{s}^{-1}$ produce poor year classes (P. Coulston, CDFG).

4.7.5 Northern anchovy

Northern anchovy (*Engraulis mordax*; Figure 41) maintain the bulk of their population in the coastal waters of California and invade the Bay on a regular, seasonal basis. Anchovies do most of their spawning outside of the Bay, although eggs and larvae are also abundant in the Bay. Adults and juveniles enter the bay in the late spring for feeding and stay until autumn.

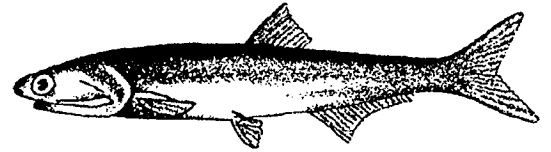


Figure 41 Northern anchovy usually 10-18 cm. (modified from Eschmeyer et al. 1983)

The northern anchovy population in San Francisco Bay has been described as a distinct subspecies (Hubbs 1925), but it seems likely that only three subpopulations are justified within the population of anchovies on the western coast of North America (Vrooman and Smith 1971). The San Francisco Bay anchovies are part of the Central subpopulation which spawns predominantly between mid-June and mid-August (Hunter and Macewicz 1980). Spawning takes place over a wide geographical range but most occurs near shore. Significant spawning within the Bay has been reported (Eldredge 1977; Wang 1986). Eggs are abundant within the Bay from May through September. However, in coastal areas nearby spawning peaks from January to April (McGowan 1986). Thus, although the population is probably not a distinct subspecies, the fish spawning in the Bay do not have the same environmental controls on recruitment success as those spawning elsewhere.

Studies of the environmental requirements of northern anchovies have not led to any clear picture of how temperature, dissolved oxygen concentrations, or depth might control their distribution or abundance (Lasker and Smith 1977; Brewer and Smith 1982). In bays they are frequently found around sewage outfalls and die-offs due to low oxygen concentrations are common (Pacific Fishery Management Council 1983). Diet of northern anchovies is very diverse. Stomachs contained mostly crustaceans and other zooplankton, but enough phytoplankton was found to suggest that it may be fed upon rather than incidentally consumed (Loukashkin 1970).

California northern anchovy populations bloomed after overfishing had removed most of the population of Pacific sardines (Baxter 1967). The fishery attempted to switch over to anchovies but after an initial heavy harvest the fish was found to be much less marketable and harvest rates declined (Skinner 1962). Extensive research was done on northern anchovy during the 1970s and early 1980s, partly in hopes of making them economically profitable without repeating the mistakes made with sardines (Spratt 1975; Hunter and Sanchez 1976; Chavez et al. 1977; Hunter 1977; Lasker and Smith 1977; Scura and Jerde 1977; Hunter and Goldberg 1980; Hunter and Macewicz 1980; Stauffer and Parker 1980; Hanan 1981; Mais 1981; O'Connell 1981; Richardson 1981; Brewer and Smith 1982; Hunter and Coyne 1982; Stauffer and Charter 1982). On the other hand, this species has been very little studied in the Bay, despite its overwhelming dominance by both number and weight (Armor and Herrgesell 1985; McGowan 1986).

Northern anchovy are the most abundant fish in San Francisco Bay. Aplin (1967) reported that northern anchovies made up 85% of the catch of 510,877 fish in Central and South bays in 1963-1966. Some of the trawls made during Aplin's study contained catches of anchovies weighing "over 1000 pounds and could not be hauled aboard." Aplin (1967) also reports seeing feeding schools of northern anchovy in South Bay which "were estimated to contain several hundred tons of fish." The bait fishery on anchovies in the Bay took about 385 tons per year during the 1970s (Smith and Kato 1979). Estimates of adult biomass calculated from egg densities suggest that in 1978-1979 peak biomass of northern anchovy was about 767 tons (McGowan 1986). Because of the large offshore population there is little concern over the impact of the Bay-based bait fishery on the total population, although little is known about the amount of fish harvested in the ocean (Smith and Kato 1979).

Embryos and larvae of northern anchovy exhibit distinctly different patterns of distribution within the Bay (McGowan 1986). McGowan's study includes only 12 contiguous months of sampling so that seasonality, per se, cannot be separated from non-seasonal changes in abundance. However, seasonality of the adult population is well documented and McGowan's conclusions generally agree with other short-term egg and larva sampling programs (Wang 1986). Eggs were found widely distributed within the Bay, while larvae showed lower densities in the stations most under the influence of oceanic water. Eggs were most abundant in areas of low zooplankton concentrations and clearer water. Stratification of the water column and warmer surfacewater temperatures also characterized stations with high egg densities. Larvae were distributed within the Bay in a complementary pattern to eggs; larvae were found in areas of high zooplankton abundance and lower water clarity. Possibly eggs survive best in regions of low zooplankton populations due to lower predation rates while larvae require high concentrations of zooplankton for feeding success.

The large population of anchovies accounts for a large predation rate on zooplankton. Adult females consume 4.5% of their body weight in zooplankton each day, and this predation may explain the lower densities of zooplankton in areas with high densities of anchovy eggs (McGowan 1986). Feeding by larvae and adults may play a role in making nitrogen available to phytoplankton; off southern California nitrogen concentrations are ten times greater in the wake of anchovy schools (McCarthy and Whitledge 1972). Consumption by adult and juvenile anchovy may account for 3,260 tons of copepods per year from the Bay. Migration to the ocean removes approximately 158 tons of new anchovy biomass from the Bay ecosystem (McGowan 1986).

Anchovies dominate the catch both of otter trawls and midwater trawls of the Bay Study. Fewer individuals are caught upstream of Carquinez Straits, but in the lower Bay northern anchovy comprise at least 70% of the number of fish caught each year. In Suisun Bay, during the first four years of the Bay study, longfin smelt outnumbered anchovies in three of the four years. Since 1984 anchovies have been the most numerous species in the midwater trawl in all embayments. In most years northern anchovy are most abundant in Central Bay, and generally more abundant in San Pablo Bay than in South Bay.

The Fall Midwater trawl survey, in the stations considered here, has only 2 of the 28 stations in the lower Bay where northern anchovies are abundant. However, the anchovy catch at those stations makes them one of the most abundantly captured fish overall.

Northern anchovies are thought to avoid surface waters during the day (Baxter 1967). However, 95% or more of the Bay Study catch of anchovies in each part of the Bay were taken in the midwater trawl. The proportion taken in the otter trawl is markedly lower for Suisun Bay.

Northern anchovies are seasonally present in San Francisco Bay. Overall they enter the Bay in April of most years and appear to outmigrate in the fall. The sharpness of their seasonality differs in the different embayments. In Suisun Bay and San Pablo Bay they peak in abundance later and disappear more rapidly than in Central and South Bay (Figure 42).

Differences of opinion exist over the effects of differing outflow regimes on the abundance of northern anchovy in the Bay (Pearson 1989). Overall, anchovies have been described as a species giving mixed response to outflow variation (Armor and Herrgesell 1985; CDF&G 1987), but in South Bay they have shown a slightly negative association with outflow (Pearson 1989). Northern anchovy abundance is largely independent among the various embayments. Spearman rank correlations of abundance across years for San Francisco Bay are non-significant for all three areas, but highest for Central and South bays (South Bay vs Central Bay $r=.65$, $p<.10$; South Bay vs San Pablo Bay $r=.22$; Central Bay vs San Pablo Bay $r=-.18$). Thus, pooling the data for all embayments may mask different use of each embayment by anchovy in different years. Responses to flow also differ across the three embayments; for both Central and South Bay there is a strong positive correlation with outflow ($r=.83$, $p<.01$ for South Bay; $r=.88$, $p<<.01$ for Central Bay). However, there is no apparent response to outflow in San Pablo Bay ($r=-.15$). These results strongly support the earlier report of a mixed response of anchovy abundance to outflow (Armor and Herrgesell 1985; CDF&G 1987a). The difference in result between the two data sets would seem to be most easily explained by the more restricted geographic scope of Pearson's study, as suggested by Pearson (1989).

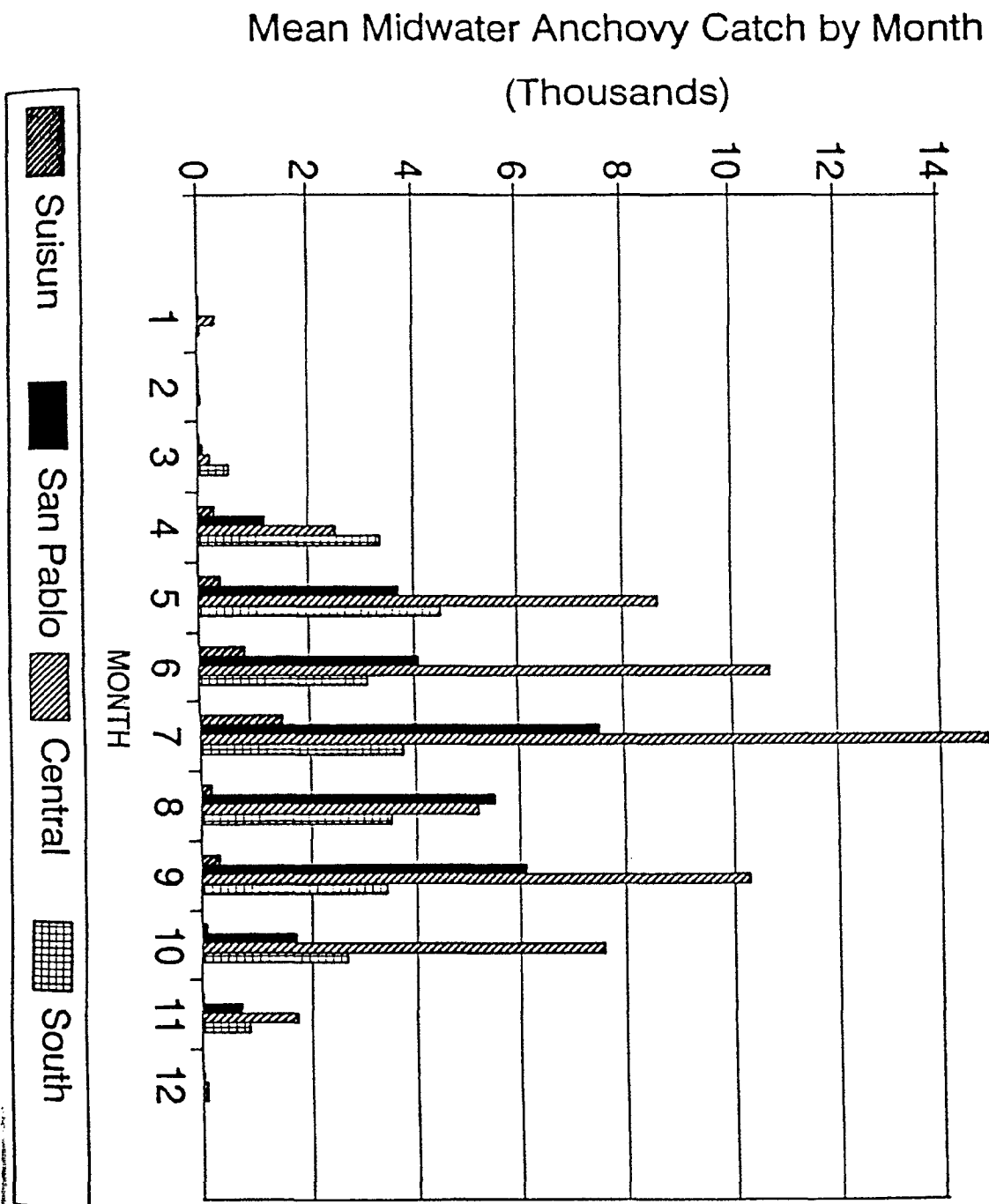
Two mechanisms seem most likely for the increased abundance of anchovy in downstream sites during wetter years: physical displacement of this surface-dwelling species by surface flows of fresh water or greater aggregation by the species during wet years in regions that are more saline. If simple transport by water currents was the motive force then high abundances downstream should be linked to lower abundance in San Pablo Bay. The absence of any effect of outflow in San Pablo Bay suggests that such displacement is not at work.

Northern anchovies have been observed spawning in the Bay (Wang 1986), but most of the population spawns in the ocean and any contribution to recruitment by Bay fishes is probably small (Stauffer and Parker 1980). Young anchovies are first caught each year in the Bay prior to or simultaneous with the catch of older fish. Thus, many of the young

ught in the Bay probably are transported in from the ocean. Anchovies are known to
own repeatedly (Hunter and Macewicz 1980) but larval anchovies appear in the Bay
arily at the start of the season (Feb-June, Mike Sullivan CDF&G pers. comm.). The
ize distribution of northern anchovies in the Bay shifted to larger fish following *El Niño* in
983 (Figure 43)

The spatial distribution of northern anchovy in the Bay between the early and late 1980s
ows no general shift (Figure 44).

Figure 42 Mean catch per month of northern anchovy in midwater nets of the Bay study 1980-88 (from data provided by DFG).



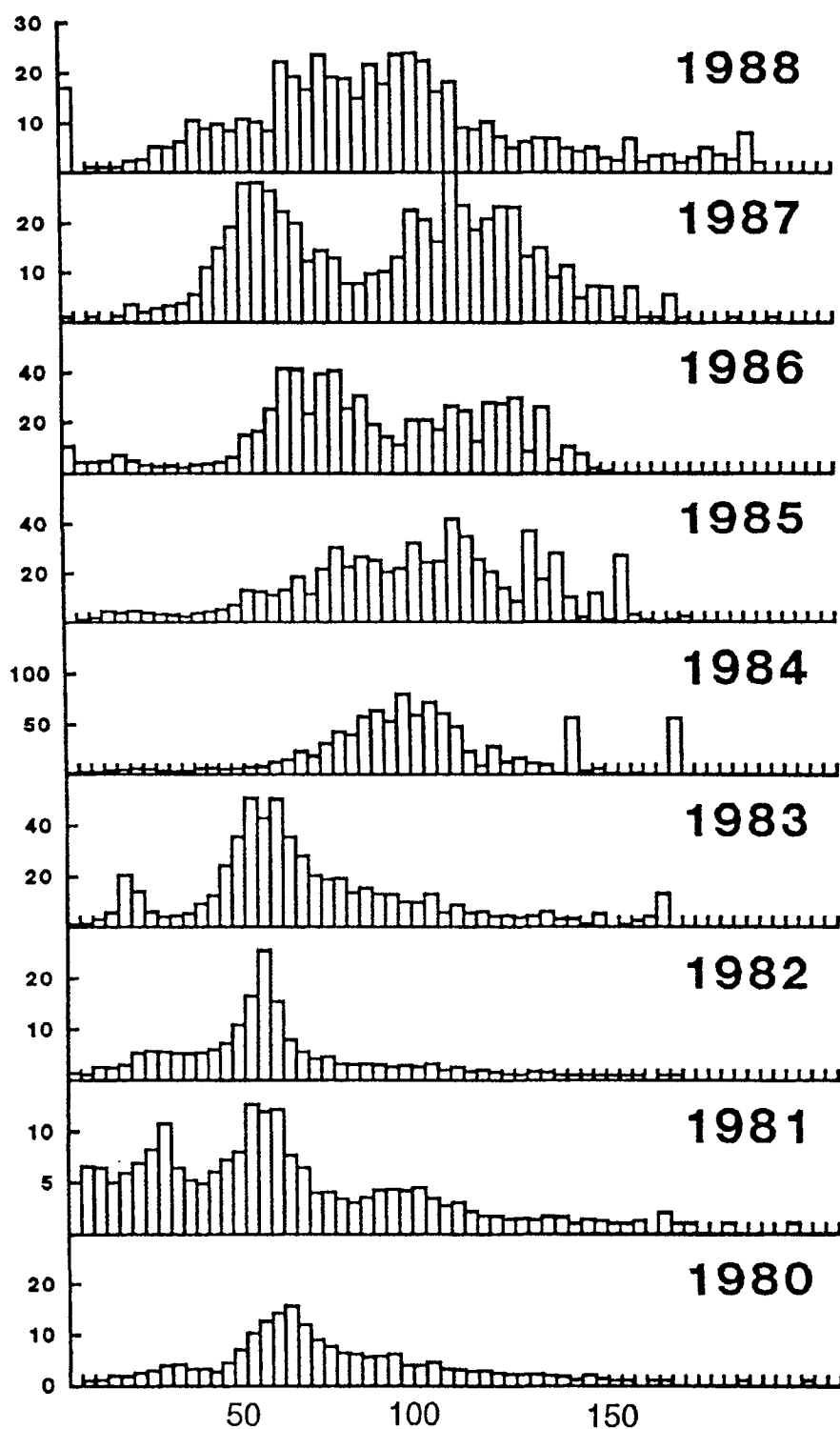


Figure 43 Length frequency histograms for northern anchovy in midwater nets of the Bay Study 1980-1988. Note elimination of small size class after 1983 and its gradual return.

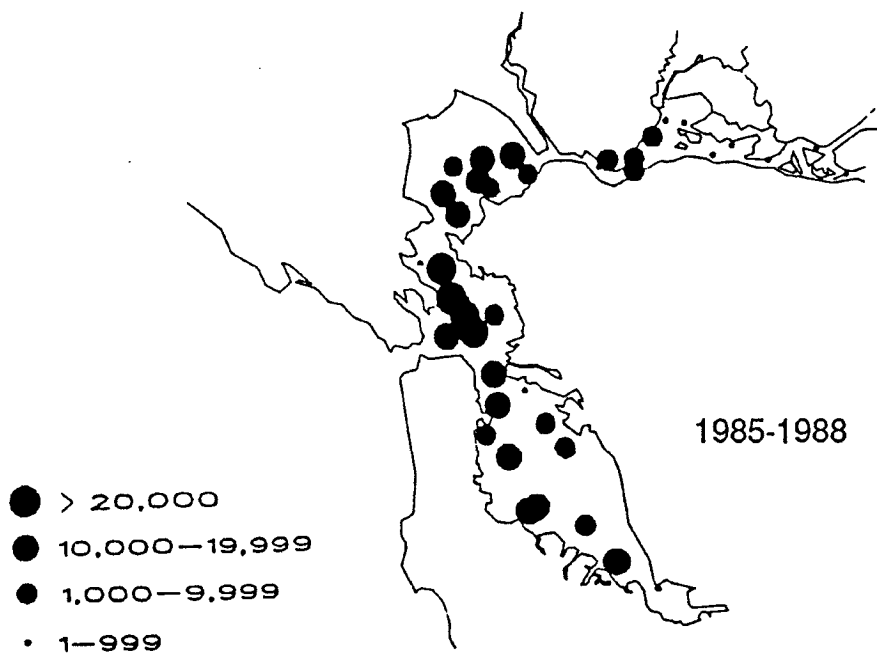
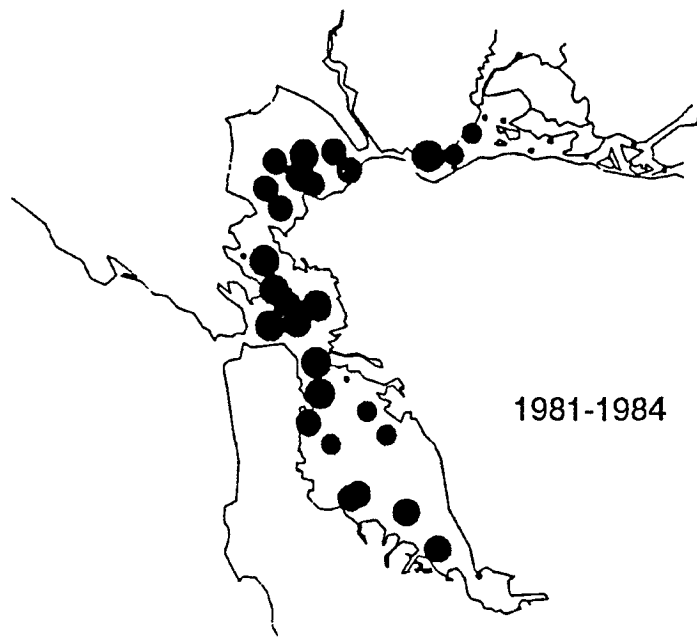


Figure 44 Distribution of northern anchovy in midwater nets of the Bay Study 1981-1984 vs 1985-1988, represented by catch at each station.

4.7.6 Pacific herring

Pacific herring (*Clupea harengus*; Figure 45) support a large fishery in the Bay, particularly for roe which is exported to Japan. Adult and juvenile herring are caught and sold for bait and some are sold fresh or canned as human food but it has never been a large fishery. As much as 3,629 metric tons were landed for a reduction fishery in 1918, but this market was eliminated by the Reduction Act of 1919 (Spratt 1981). As with northern anchovy,

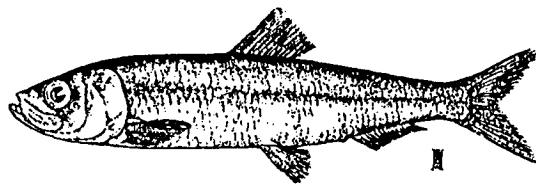


Figure 45 Pacific herring, usually 20-30 mm. (from Moyle 1976)

an attempt was made in the 1940s and 1950s to substitute herring for the failing sardine fishery but the efforts met with little consumer acceptance. The roe fishery consists of two separate harvests (Spratt 1981). Divers collect eggs after they have been deposited on *Laminaria* or *Gracilaria*, to be sold in Japan as 'kazunoko kombu.' Spawning adults are caught mostly in gill nets in order to select the largest individuals, and the ovaries of the ripe females are taken to be sold in Japan as Kazunoko. Gonadal weight in ripe herring approaches 22% of body weight (Hay and Fulton 1983). The roe fisheries began in 1972 and instigated the first scientific studies of herring in California (Spratt 1981).

Although herring appear to be very adaptable to changing conditions on the spawning grounds, there is a need to identify what ecological features might explain the history of collapses that have characterized herring fisheries (Doubleday 1985). The Baltic Hanseatic League of the 16th century provides the earliest example of a collapsed herring fishery (Blaxter 1985). Recruitment appears to be the limiting stage on herring abundance (Doubleday 1985), so fisheries such as that for Kazunoko may be most likely to affect abundance. Herring are flexible and resilient so that, even where overfishing has destroyed a fishery, it may be possible to restore the population (Blaxter 1985; Ware 1985). In San Francisco Bay, where the population is still thriving, possibilities for effective management seem good if harvest rates stay below quotas or if a better understanding of the biology of the species permits the application of scientifically based quotas.

San Francisco and Tomales Bays attract the largest spawning aggregations of herring in California (Spratt 1976). Adults begin migrating into bays one to two months before actually spawning (Miller and Schmidtke 1956). In San Francisco Bay immigration begins in November and spawning generally occurs between December and February (Wilson 1937; Scofield 1952; Spratt 1981). The size of the spawning population has been relatively stable, with the largest variation associated with *El Niño* conditions of 1976-1977 and 1983 (Table 3). The decline in biomass of 1976-77 was accompanied by greater than usual spawning biomasses in Tomales Bay. The decline in catch during 1983 was apparently part of a reduced oceanic population of herring in response to reduced productivity. Reasons for the general increase of herring abundance through time, despite increasing commercial catch, are unclear.

Adults begin to move toward their spawning grounds in autumn; spawning in San Francisco Bay generally begins in November and continues through March (DFG 1991). Juvenile abundance within San Francisco Bay has been strongly correlated with recruitment to the adult spawning population two years later. However, the most recent year for which there are data produced a strong discrepancy between actual recruitment and that expected from the earlier index of young-of-year abundance (Oda and Wendell 1990). Smaller young tend to be widely distributed in shallower habitats in South, Central and San Pablo Bays. As the young grow they are found in deeper waters closer to the Golden Gate and most emigrate from the Bay between April and August (M. Sullivan CDF&G pers. comm.).

Table 3. Estimated spawning biomass of Pacific herring in San Francisco Bay. Data prior to 1980 from Spratt (1981), estimates after 1980 from personal communication with J. Spratt, CDF&G Marine Resources Division.

Spawning season	Estimated spawning biomass (thousands of metric tons)
1974-1975	27
1975-1976	25
1976-1977	22
1977-1978	4
1978-1979	33
1979-1980	46
1980-1981	65
1981-1982	99
1982-1983	59
1983-1984	41
1984-1985	47
1985-1986	49
1986-1987	57
1987-1988	69
1988-1989	66
1989-1990	71

Pacific herring spawn in a very restricted area of San Francisco Bay. Most of the spawning occurs in intertidal and shallow habitats of the Tiburon Peninsula and Angel Island although some spawning occurs on aquatic vegetation near Berkeley and Richmond (Spratt 1981). Herring will not spawn over the mud substrates that characterize much of the shallow, intertidal habitat on the east side of the Bay. The apparent transferral of spawning to Tomales Bay for the 1977-78 season suggests that, despite the restricted spawning requirements and tendency for races to return to natal sites, herring will likely respond to habitat loss in the Bay by using other coastal sites.

4.7.7 American shad

American shad (*Alosa sapidissima*; Figure 46) populations rapidly increased following their planting in 1871 (Love 1991). The semi-buoyant eggs probably reduced the impact of siltation on egg mortality, and the use of river channels for spawning, rather than small tributary streams like salmonids, probably also gave them a much better chance to successfully spawn in spite of the effects of hydraulic mining. Eight years after planting, American shad supported a commercial fishery and

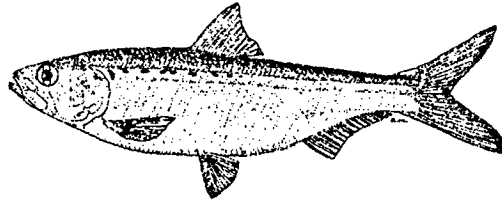


Figure 46 American shad, adults to 70 cm, juveniles in the Delta are less than 20 cm (from Moyle 1976).

rapidly spread to all other estuaries from Alaska to Baja California (Fry 1973). Their spread was facilitated by additional introductions into other estuaries, but their spread throughout the region and as far away as Kamchatka underscores the great degree to which this fish moves in the ocean. Maximum size of adult American shad is 760 mm and many of the spawning fish weigh 2 to 3 kg. Runs of American shad in the Sacramento River have been estimated at 3.04 million fish in 1976 and 2.79 million in 1977, but populations in the early part of this century were likely 2 to 3 times as large (Stevens et al. 1987). American shad spawn for the first time at ages ranging from two to five years; about 70% of the fish spawning in any year are first-time spawners (R. Painter 1979, unpublished report, CDF&G).

American shad are oceanic as adults except for a brief spawning run in fresh water. Most central California adults spawn in the Sacramento River or its tributaries; spawning in the Delta or San Joaquin River accounts for little of the recruitment (Stevens 1966). Spawning migrations begin in March with the peak of spawning in late May or June (Stevens 1966a). Within their native range American shad seldom eat while on the spawning migration, but in the Sacramento-San Joaquin estuary they continue to feed as they pass through the Bay and generally cease feeding in fresh water (Moyle 1976). Most young American shad rapidly migrate downstream after hatching and most are gone by December, but a few can remain as long as a year. Many adults die after spawning, but some return to the ocean and spawn again in later years.

The CDF&G sampling programs do not encompass many of the times or places of American shad abundance. By the time of the Fall Midwater trawl survey most young shad have already begun their migration out of the Delta. The significance of the place and timing of this is revealed in the fact that the greatest catch of American shad in the Fall Midwater trawl survey occurs in September and declines least rapidly in Suisun Bay (Table 4), the first sampling month and the most downstream location. The Bay Study does not sample in the Delta where American shad are most concentrated and where most mortality of young fish occurs. The peak catch in Bay Study trawls occurs in August or September of all years, which reinforces the suspected bias of the Fall Midwater Trawl survey. Catch of American shad in Suisun Marsh is very low (Moyle et al. 1985). Midwater and otter trawls

used in this study are poor sampling gear for larger fish. More than 99% of the American shad caught by the Bay Study were young of year (<170 mm total length). Lengths are not available for most years of the Fall Midwater Trawl survey, but the timing of the trawls almost ensures the absence of adults. No recent estimates of spawning numbers seem to exist.

Despite these biases it is still possible to determine some patterns in the data. Stevens and Miller (1983) describe the apparent increase in American shad recruitment in wetter years. Recent data confirm the earlier study. Lower catches of American shad have generally occurred during drought periods, 1976-77 and 1985-1988 (Figure 47). American shad captures in the Bay Study fluctuate during the first four years and are not lowest in 1981, although that was a dry year. The four lowest catches of American shad by the Bay Study occurred in the last four years, which were all dry (Table 5).

Table 4. Mean catch of American shad in fall midwater trawls. All trawls included.

	Sacramento River	San Joaquin River	Suisun Bay
September	6.6	13.8	7.22
October	4.7	7.5	65.99
November	4.9	5.1	75.42
December	2.4	1.9	22.54

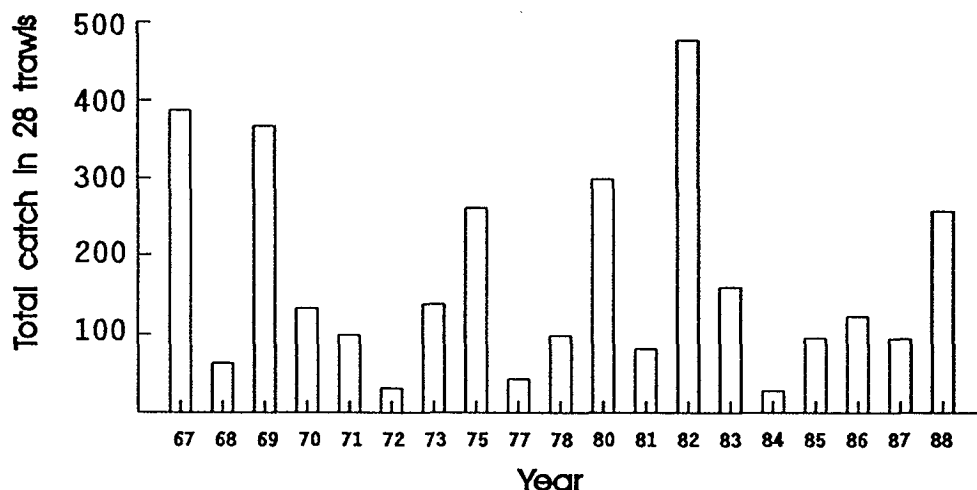


Figure 47. Catch of American shad in September trawls of the CDF&G Fall Midwater Trawl survey.

Table 5. Catch of American shad in trawls of the CDF&G Bay Study.

	80	81	82	83	84	85	86	87	88	Overall
January	18	28	7	22	5	13	5	16	7	121
February	16	42	3	12	4	17	10	7	2	113
March	13	14	1	2	2	6		2	2	42
April	2	13	2	1	6	1	2	4	3	34
May		13	11	1			1	4		30
June	3		6				2	1	1	13
July	9		86	6	121			5	31	258
August	41	30	506	79	60	18	14	21	63	832
September	14	59	220	281	40	20	36	26	13	709
October	44	92	205	84	23	25	63	18	24	578
November	23	36	172	51	14	16	17	8	17	354
December		7	48	23	10	15	15	11	12	141
Total for Year	183	334	1267	562	285	131	165	123	175	3225

The mechanism most likely to explain the linkage of American shad abundance with outflow is that temperatures over 20 C are known to produce high mortality in young shad. Drought conditions are often accompanied by increases of temperature in the smaller volume of water so that young shad are stressed. This effect is likely most effective within the Delta or upstream because temperatures recorded from Suisun Bay during the months of American shad abundance show no upward shift through time (Table 6). However, increased entrainment during dry years probably also contributed to the decline.

Table 6. Mean temperatures (C) in Suisun Bay for each month and year of the Bay Study.

	80	81	82	83	84	85	86	87	88	mean
Jan	9.3	10.4	7.5	6.9	9.0	7.9	8.4	8.9	7.0	8.3
Feb	12.6	10.9	8.9	9.9	10.5	8.6	11.2	9.1	9.5	9.8
Mar	14.4	14.4	11.9	12.2	12.4	11.9	13.4	11.6	13.9	12.7
Apr	16.7	15.3	14.0	13.1	13.9	13.8	16.1	15.2	17.0	15.0
May	17.6	18.1	16.5	15.0	17.3	16.6	16.1	20.0	15.6	17.0
Jun	19.4	21.6	18.2	20.2	19.2	21.3	18.9	19.7	17.9	19.6
Jul	21.0	21.1	21.2	22.2	22.7	21.3	21.0	20.8	21.1	21.5
Aug	19.5	20.7	21.3	22.1	22.5	20.0	19.7	21.2	20.4	21.0
Sep	20.2	19.5	20.1	22.5	21.9	19.7	18.8	20.7	19.0	20.4
Oct	16.7	18.5	18.9	19.3	19.8	18.6	17.5	19.3	17.7	18.6
Nov	10.9	16.1	14.7	17.6	14.6	15.4	16.0	17.2	16.0	15.7
Dec	11.8	10.6	10.0	10.1	10.5	12.1	12.8	11.8	11.2	
All	16.3	16.2	14.0	16.2	16.4	15.3	15.7	16.3	15.4	15.7

4.7.8 Delta smelt

Delta smelt (*Hypomesus transpacificus*; Figure 48) are confined to the upper Sacramento-San Joaquin estuary. They have been proposed for endangered status, and the information here is condensed from supporting documents for the petition (Stevens et al. 1990; Moyle et al. 1991).

Historically, the upstream limits of their range have been around Isleton on the Sacramento River and Mossdale on the San Joaquin River, with the lower limit being Suisun Bay (Radtke 1966b; Moyle 1976; Lee Miller, CDF&G, reports catching Delta smelt above Sacramento). It seems likely that, prior to the reclamation of Delta islands, Delta smelt occurred much further upstream. Their small mouths and rather restricted diet on copepods suggest that Delta smelt feed by picking individual food items from the water column. When the Delta was more productive food may have been dense enough to allow Delta smelt to feed over a wider range; their present concentration in the entrapment zone may simply mean that it is the only remaining area with dense enough populations of copepods to permit these fish to harvest enough to keep alive.

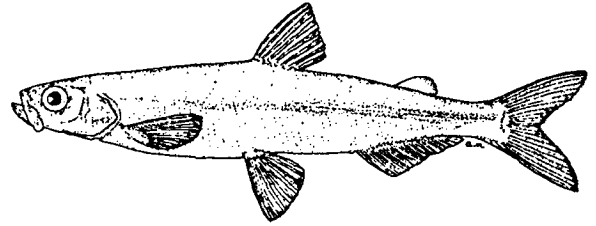


Figure 48 Delta smelt, adults usually 7-8 cm. (from Moyle 1976)

Prior to their sharp decline in abundance after 1984, Delta smelt concentrated in shallow-water areas near the entrapment zone or in the river channels immediately above it, except when spawning. In Suisun Bay, 62% of the smelt were captured at three stations less than 4 m deep; 38% were captured at six stations greater than 4 m deep. The shallow depth preference of Delta smelt is most apparent when compared with longfin smelt which show a reverse pattern of distribution, arguing that catch at one depth is not simply a result of greater trawl efficiency in shallow water. Most smelt were also caught upstream of areas where there was a large difference between surface and bottom specific conductances or in the channels of the lower Sacramento and San Joaquin rivers (Figure 49). They were rarely caught in similar areas in San Pablo Bay where the water was more saline than in upstream areas.

During times of exceptionally high outflow from the rivers, Delta smelt may be washed into San Pablo Bay, but they do not establish permanent populations there (Ganssle 1966). Delta smelt inhabit surface and shoal waters of the main river channels and Suisun Bay where they feed on zooplankton. Stevens and Miller (1983), did not find any relationship between smelt abundance and outflow.

The mean monthly catches of Delta smelt in the Fall Midwater trawl survey vary from month to month and from year to year; an additional survey for juveniles in the Summer shows a very similar pattern (Figure 50). However, some trends are evident. From 1967 through 1975, fall catches were generally greater than 10 smelt per trawl per month (6 of 8 years); from 1976 through 1989 catches were generally less than 10 smelt per trawl per month (13 of 14 years). Since 1986, catches have averaged considerably less than 1 smelt

per trawl per month. The Bay Study and Suisun Marsh study show sharp declines in Delta smelt at about the same time.

Overall, Delta smelt concentrate near or immediately upstream of the entrapment zone. Comparing the overall patterns of stratification in Suisun Bay for the period prior through 1984 to data from the same stations after 1984 shows a general difference in location of the entrapment zone. In the earlier period the entrapment zone was located in Suisun Bay during October through March except during months with exceptionally high outflows or during years of extreme drought. During April through September they were found usually upstream, in the channels of the rivers. Since 1984 the entrapment zone, just upstream of the stratified water column, has been located mainly in the channels of the rivers during all months of the year (Figure 51). In Figure 49 the heights of the bars indicate the difference in average salinities measured at the surface and at the bottom; a large difference indicates a stratified water column with a layer of fresh water overlaying the bottom salt water layer. The upstream limit of stratification, where there is no difference between surface and bottom salinities, indicates the position of the entrapment zone. The line indicates mean catch per trawl at each station. Notice that in the later 4 years the entrapment zone is generally upstream of its location in the first four years. This shift in the location of the entrapment zone during the winter months coincides with an upstream shift and narrowing of the location of the Delta smelt population to the deeper water of the main river channels (Figure 51).

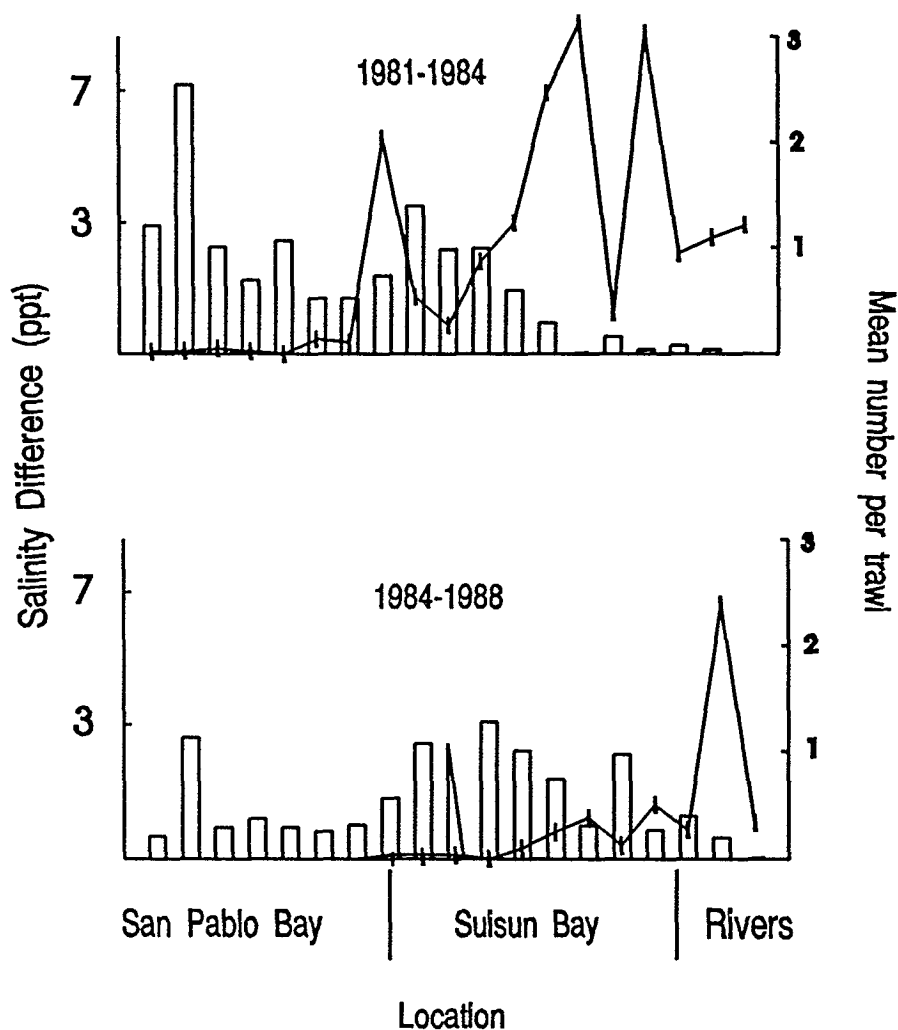


Figure 49. Salinity stratification and abundance of Delta smelt at Suisun Bay stations the period from May to October. Bars give difference in conductivity between surface and bottom, line gives mean Delta smelt capture.

The frequency of occurrence of Delta smelt in the trawls has also declined. Prior to 1983, Delta smelt were found in 30% or more of the fall trawl catches. In 1983-85, they occurred in less than 30% of the catches, and from 1986 onwards they have been caught in less than 10% of the trawls. The trend of a dramatic decline in Delta smelt numbers after 1982 is also reflected in the total catch data, although sampling efforts have been higher since 1980. This trend is reflected as well in the annual catch data from two other studies for which effort was more or less constant. The exact timing of the decline is different in most of the sampling programs but falls between 1982 and 1985. Length-frequency data validates earlier studies, showing that the Delta smelt is primarily an annual species, although a few individuals may survive a second year.

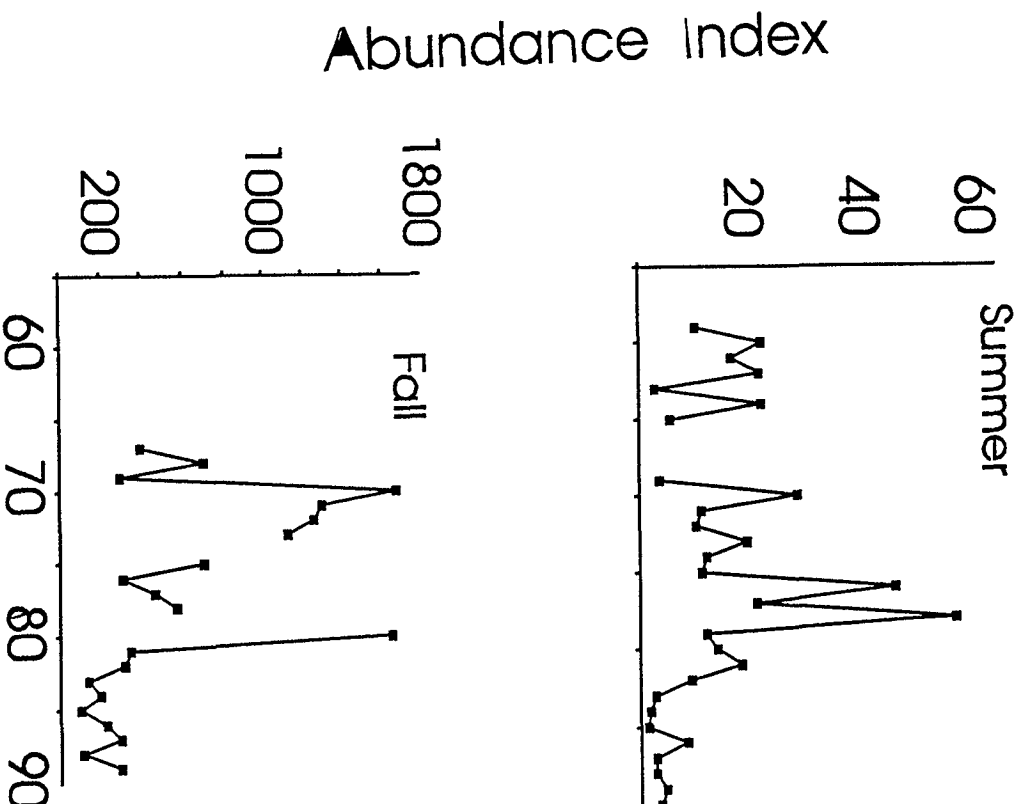
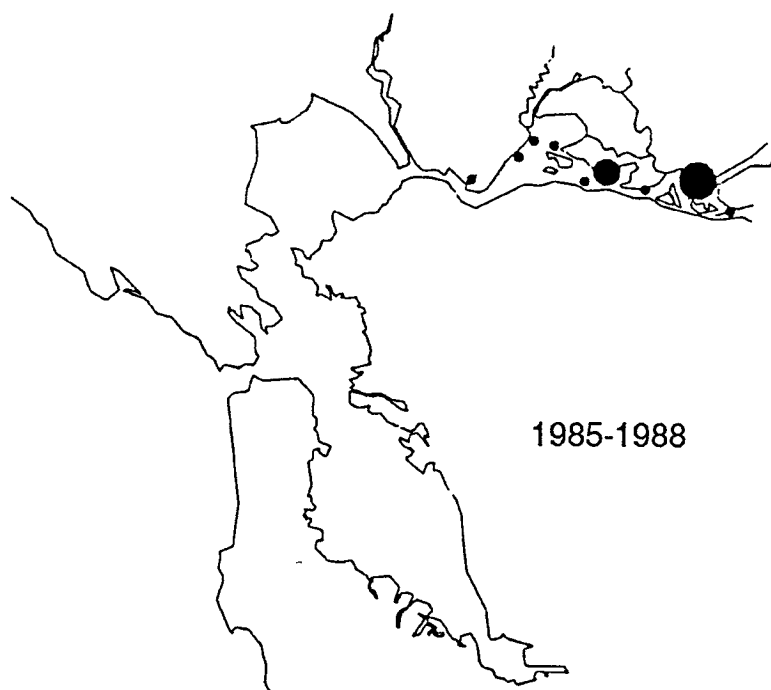
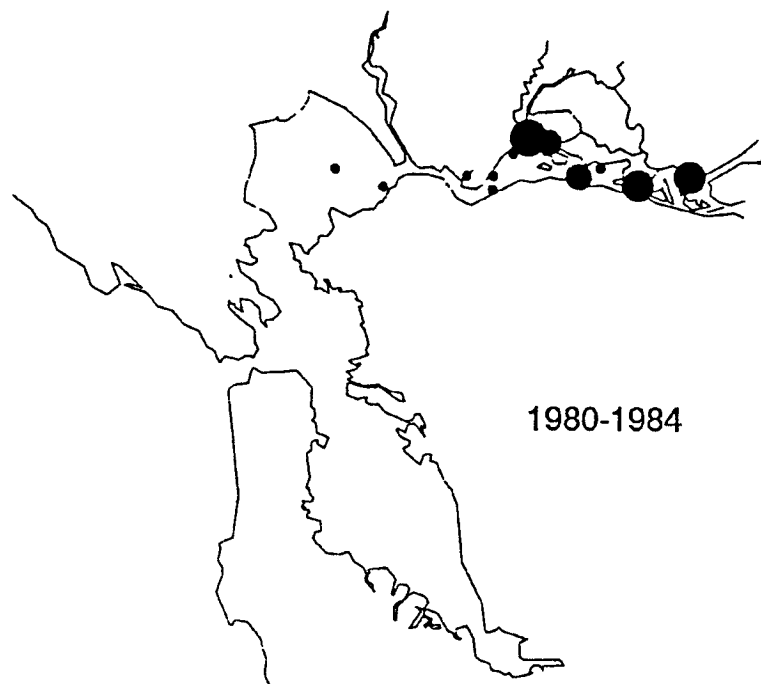


Figure 50. Index of abundance for Delta smelt from the Summer Trawl Survey and Fall Midwater Trawl Survey.

Captures of larval Delta smelt indicate that spawning can take place in fresh water any time from late February through May, when water temperatures are from 7 to 15°C (Wang 1986), although most spawning occurs in March and April. Spawning occurs in shallow water along the edges of the rivers and adjoining sloughs (Radtke 1966b, Wang 1986) but spawning behavior has not been observed. Delta smelt embryos are demersal and adhesive, sticking to hard substrates such as rocks, gravel, and tree roots (Moyle 1976, Wang 1986). Hatching occurs in 12-14 days, if development rates of the embryos are similar to those of the closely related wagasaki, *H. nipponensis* (Wales 1962).



- 31-43
- 21-30
- 11-20
- 1-10

Figure 51 Map of delta smelt distribution in the period from May to October for the two time periods 1980-1984 and 1985-1988.

After hatching, the buoyant larvae are carried by currents downstream into the entrapment zone of the estuary where incoming saltwater mixes with outflowing fresh water. The mixing currents keep the larvae circulating with the abundant zooplankton that also occur in this zone. Growth is rapid and the juvenile fish are 40-50 mm fork length (FL) by early August (Erkkila et al. 1950, Ganssle 1966, Radtke 1966b). Delta smelt become mature when 55 to 70 mm FL and rarely grow larger than 80 mm FL. Delta smelt larger than 50 mm FL become increasingly rare in samples in March through June, so presumably most adults die after spawning, completing their life cycle in one year (Erkkila et al. 1950; Radtke 1966b).

The fall midwater trawl data census only the adults, but since the bulk of the population, not the entirety, lives only one year this accurately reflects total recruitment from the previous season's spawning.

Four major factors were examined in relation to smelt distribution and abundance: electrical conductivity (specific conductance), temperature, depth, and freshwater outflow. Conductivity was regarded as particularly important because it is a measure of salinity that is highly correlated with other variables such as turbidity and productivity and was used to track the mixing (entrapment) zone. At each sampling station, specific conductance (and salinity) and temperature were measured with a salinity-conductivity-temperature meter at the surface. To determine the location of the mixing (entrapment) zone, we used specific conductance data collected monthly since January 1981 by the Bay Study, in which specific conductance at both the surface and bottom was measured. The large difference between the two measurements indicated the presence of stratification, as incoming fresh water is less dense than tidal salt water. A small difference in specific conductance indicated a well-mixed water column or stations located entirely in fresh water.

Movement of the entrapment zone into Delta channels is a result of low Delta outflow, which is calculated primarily from the sum of Delta inflows minus the water diverted and used within the Delta. Since 1983, the proportion of the water diverted during October through March (first half of the official water year) has been higher than in most earlier years. Because high levels of diversion draw Sacramento River water across the Delta and into the channel of the San Joaquin River downstream of the pumps, the lower San Joaquin River has a net flow upstream during these periods (Figure 52; actual flow at a particular moment is a function of outflow and tidal action). The number of days of net reverse flow of the San Joaquin River has consequently increased in recent years, especially during the months when Delta smelt are spawning (Figure 53). The decline in Delta smelt coincides with the increase in proportion of water diverted since 1983 and the confining of the entrapment zone to a small area in the channels of the lower rivers. Other major changes in estuarine conditions (increased toxic loads and explosive spread of introduced species) did not happen at the same time as the decline of Delta smelt and are therefore less likely to have been the cause. Determination of causality, however, cannot be done without experimental manipulation of diversion schedules.

The Delta smelt is a species that is best suited for living near the entrapment zone of the Sacramento-San Joaquin Estuary where it feeds on the concentrations of copepods and other zooplankton there. When the entrapment zone is located in Suisun Bay, optimal conditions for smelt occupy a much larger total area that includes extensive shoal areas than when the entrapment zone is located upstream in the Delta. The river channels in the Delta are comparatively small in surface area and have few shoal areas, so are less favorable to the Delta smelt. Because the Delta smelt is essentially an annual fish with relatively low fecundity, a large entrapment zone with extensive shallow areas immediately downstream from its spawning areas must have been a predictable part of its environment during much of the smelt's evolutionary history. Increasing diversions of fresh water from the estuary have altered the location of the entrapment zone, as well as the flow patterns of the Delta during most months of the year. The movement of the entrapment zone to the river channels not only decreases the amount of area that can be occupied by smelt but probably results in decreased phytoplankton and zooplankton as well (Herbold and Moyle 1989; Appendix A). During the months when Delta smelt are spawning, the changed flow patterns presumably draw larvae from the Sacramento River into the San Joaquin River, where they can be exported through the pumps along with locally produced larvae.

Entrainment or dislocation of larvae by exportation of water has no doubt been exacerbated by the near-drought conditions that have existed in the drainage since 1987, coupled with the record high outflows that occurred in February 1986 (which may have flushed fish out of the estuary). However, since 1984 the percentage of inflow diverted has been higher and stayed higher for longer periods of time than during any previous period, including the severe 1976-77 drought.

Although the recent high diversions of fresh water coupled with drought conditions are the most likely cause of the precipitous decline in the Delta smelt population, other factors that may be contributing are (1) toxic compounds in the water, (2) displacement of native copepods by exotic species, and (3) invasion of the estuary by the euryhaline clam, *Potamocorbula amurensis*. Pesticides in the Sacramento River at concentrations potentially harmful to larval fish and zooplankton have been recorded in recent years by the Central Valley Regional Water Quality Control Board (C. Foe, personal communication). The effects of these pesticides on smelt is unknown, but they have occurred at high levels in fresh water prior to the most recent decline of the smelt. The concentration of smelt in the entrapment zone may have allowed them to avoid the effects of pesticides, because of the dilution of the contaminated fresh water by inflowing seawater.

Increases in the abundance of two exotic copepod species have been associated with a reduction in the abundance of *Eurytemora affinis*, principal food of the Delta smelt. The invasion of *Sinocalanus doerri* occurred prior to the smelt decline, although the invasion of *Pseudodiaptomus forbesi* apparently occurred around 1986. Although *S. doerri* is apparently rarely eaten by Delta smelt, *P. forbesi* is now a major part of their diet. Meng and Orsi (1919) have found that larval striped bass readily take *P. forbesi* but have a difficult time

capturing *S. doerri*. Despite this, it does not appear that the shift in copepod species has had a major impact on Delta smelt populations because the smelt have shifted their diet as well.

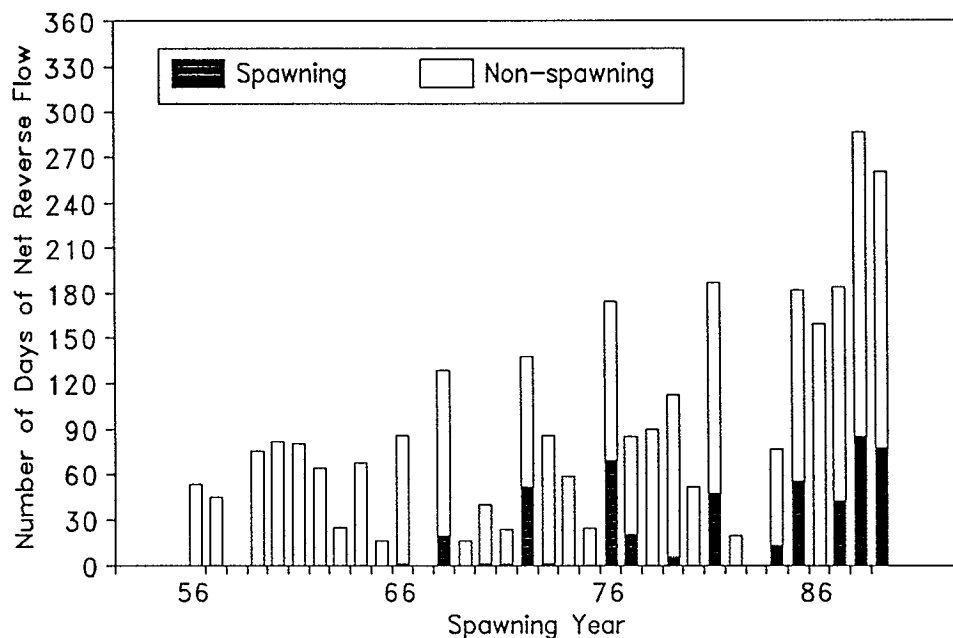


Figure 53. Number of days in each year when net flow was reversed in lower San Joaquin River. Time of Delta smelt spawning indicated as solid bar.

4.7.9 Longfin smelt

Longfin smelt (*Spirinchus thaleichthys*; Figure 54) are small planktivores found in several Pacific coast estuaries from Prince William Sound, Alaska to San Francisco Bay. Until 1963 the population in San Francisco Bay was thought to be a distinct species, the Sacramento smelt. Northern populations were originally described as a different species (*S. dilatatus*, Schultz and Chapman 1934), but the identifying characteristics were shown to follow a gradient and the two species were merged (McAllister 1963). Although studies in other estuaries are scanty, it appears likely that the population in San Francisco Bay has been the largest population. Within California, longfin smelt have been reported from Humboldt Bay and the mouth of the Eel River but there are no recent records from the Eel River and it is infrequently collected in Humboldt Bay (R. Frizsche, pers. comm.).

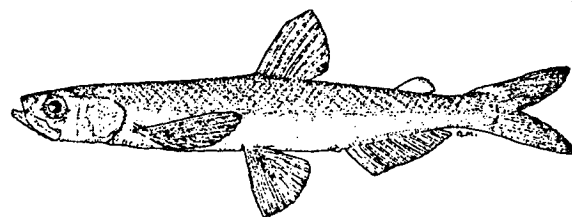


Figure 54 Longfin smelt, adults usually 9-10 cm. (from Moyle 1976)

Longfin smelt differ substantially from Delta smelt. Consistently, a measurable portion of the longfin smelt population survives into a second year. The larger mouth of the longfin smelt reflects the greater proportion of large zooplankton in their diet--particularly the opossum shrimp (Moyle 1976; Wang 1986; Herbold 1987). Adult longfin smelt are broadly distributed throughout the estuary.

Because longfin smelt seldom occur in fresh water except to spawn but are widely dispersed in brackish waters of the Bay, it seems likely that their range formerly extended as far up into the Delta as salt water intruded. Prior to construction of Shasta Dam, salt water would invade the Delta as far upstream as Sacramento during dry months. Similarly, Delta smelt appear to require denser concentrations of zooplankton than the hydrology of the Delta now permits. Thus, the development of agriculture and water projects probably restricted the ranges of both species before any studies of their biology were begun.

The primary ecological similarity between the two smelt species is that they both spawn in river channels at the easternmost end of the San Francisco Bay complex. In both species the adhesive eggs hatch after a few days and currents normally transport the larvae downstream. If changes of flow in the spawning ground are the mechanism by which the Delta smelt populations have suffered decimation, then the same pattern can be expected in longfin smelt populations.

Although longfin smelt populations were known to be affected by freshwater inflow to the estuary (Stevens and Miller 1983), there has been little concern for their persistence in the estuary as they have been regarded as abundant and widely distributed, with additional populations in other California estuaries (Moyle 1976; Monaco et al. 1990). A recent

compilation of fish species of special concern for California, for example, does not list them (Moyle et al. 1989).

As reported from the general descriptions of their biology (Moyle 1976; McGinnis 1985; Wang 1986), longfin smelt in the records of CDF&G are more broadly distributed in the Bay. They are found at higher salinities than Delta smelt. The easternmost catch of longfin smelt in the Fall Midwater trawl was at Medford Island in the Central Delta. They have been caught at all stations of the Bay Study. A pronounced difference between the two species in their region of overlap in Suisun Bay is by depth; longfin smelt are caught more abundantly at deep stations (> 10 m) whereas Delta smelt are more abundant at shallow stations (< 3 m).

In both South Bay and Central Bay, a brief dominance by longfin smelt occurs in the midwater catch in 1983. In San Pablo and Suisun Bay their abundance in 1983 was lower than their abundance in 1982, thus supporting the idea of washout from upstream.

Unlike Delta smelt, longfin smelt have a measurable portion of their population survive into a second year. In addition, there is a significant difference in the distribution of longfin smelt of different sizes. After hatching, young longfin smelt are most abundant in the otter trawls of San Pablo Bay and larger fish are generally caught in midwater trawls in Suisun Bay. This difference is most pronounced immediately after spawning but the difference in size for each month for the two nets is significant for all but one month of the year (Figure 55). Whereas longfin smelt are segregated from Delta smelt in Suisun Bay by their use of deeper stations and greater occurrence in the otter trawl, in San Pablo Bay they occur more commonly in the midwater trawl. Comparing the catch of each net through time in each embayment shows that longfin smelt have nearly disappeared from San Pablo Bay and from the otter trawl (Figures 55 and 56). A procedural shift in the minimum size at which longfin smelt were included in the catch causes the catches not to be strictly comparable across years; the data presented in figures 55 and 56 are only for those fish that were greater than 100 mm in length, all fish of this size were counted in all years.

Longfin smelt populations in the 1980s have followed a trajectory similar to that shown by Delta smelt. Abundance was high in 1980, low in 1981, high again in 1982, and in sharp, continuous decline from 1983 through 1988. The decline in 1981, a dry year for which Delta smelt remained at relatively high numbers, reflects their dependence on high outflows described by Stevens and Miller (1983). Longfin smelt failed to recover in 1986, nominally a wet year, because record flows in February presumably flushed a high percentage of mature adults out of the Estuary.

Unlike Delta smelt, which declined in frequency of occurrence but not in abundance at the stations at which they are still caught, longfin smelt have retained most of their earlier distribution but their catch at each station has declined (Figure 58).

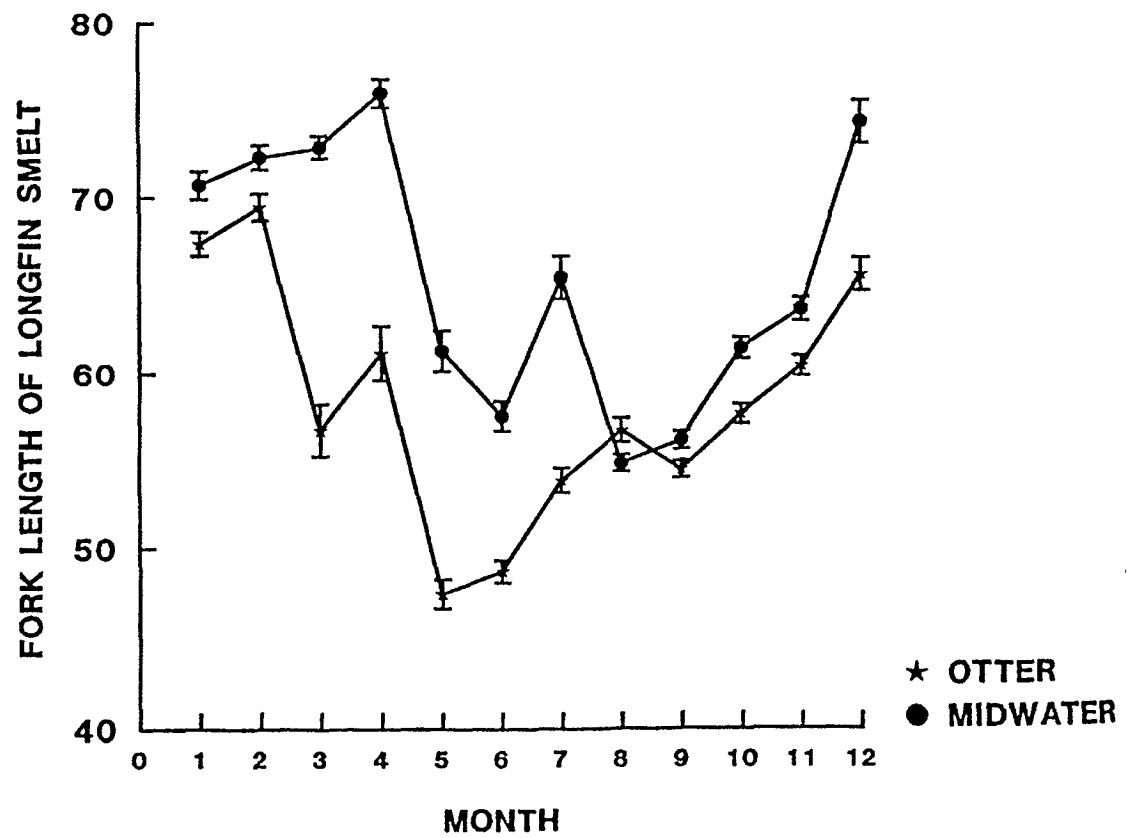


Figure 55 Differential capture of longfin smelts of different sizes in the midwater and otter trawls of the Bay Study.

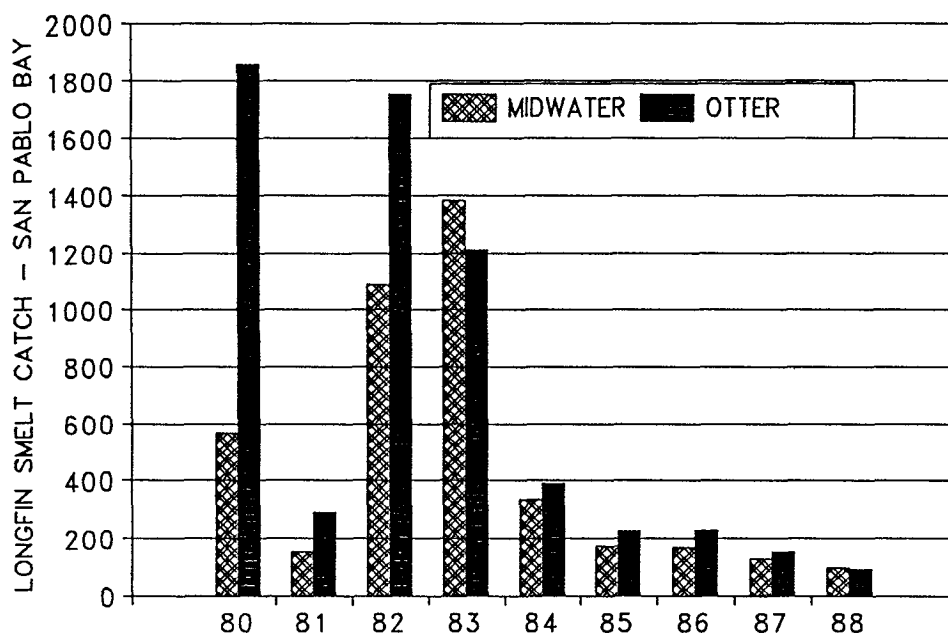


Figure 56 Decline of catch of longfin smelt (> 40 mm fork length) in the midwater and otter trawls in San Pablo Bay (data from CDF&G Bay Study).

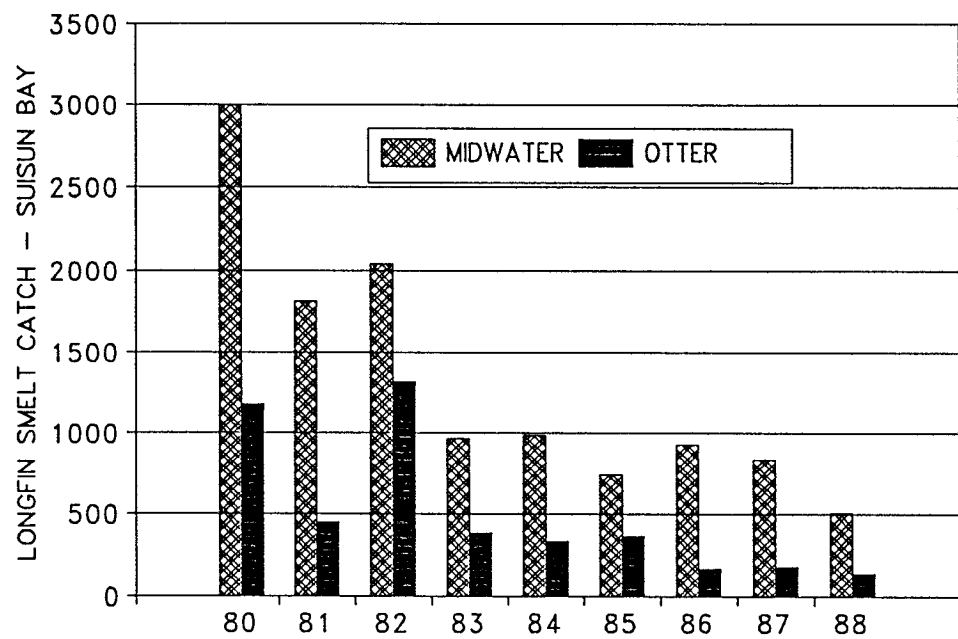


Figure 57 Decline of catch of longfin smelt (>40 mm fork length) in the midwater and otter trawls in Suisun Bay (data from CDF&G Bay Study.)

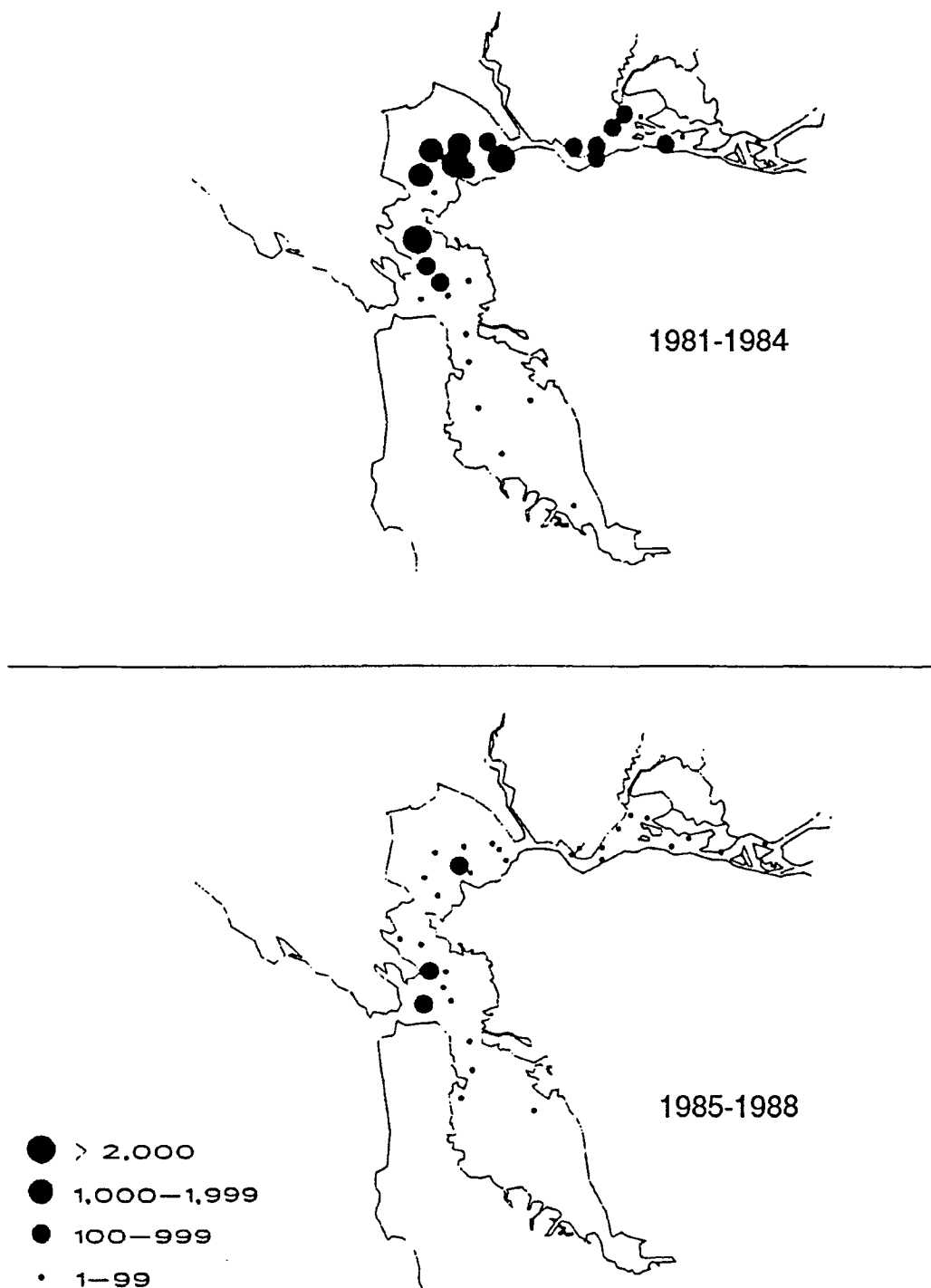


Figure 58 Distribution and abundance of longfin smelt at each of the consistent sampling sites of the Bay study.

5.0.4 Threadfin shad

Threadfin shad (*Dorosoma petenense*; Figure 59) were introduced from Tennessee into the Sacramento-San Joaquin River system in 1953 to provide a forage base for largemouth bass in reservoirs (Burns 1966). Downstream spread introduced the species into the Delta where it is abundant.

Threadfin shad are a relatively minor component of striped bass diet (Moyle 1976). Shad usually occur in more-or-less even aged schools, with schools of young frequently living in deeper, more open-

water habitats than adults (Johnson 1970). Feeding appears to be relatively non-selective on planktonic crustacea (Turner 1966, Miller 1967). The extremely long and fine gill rakers collect a wide variety of plankters and the presence of a thick-walled muscular crop permits digestion of all kinds of zooplankton. Threadfin shad seldom exceed 100 mm total length.

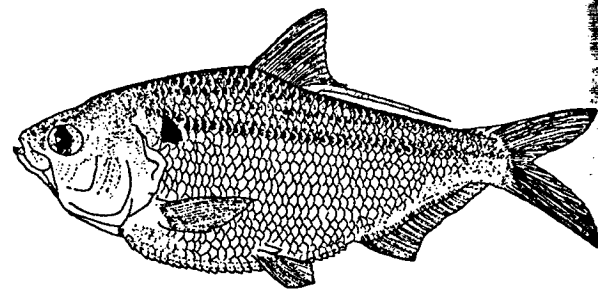


Figure 59 Threadfin shad, adults usually less than 10 cm. (from Moyle 1976)

Threadfin shad spawn in the late spring and on through the summer (Johnson 1971; Moyle 1976). The demersal and adhesive eggs are often laid on drifting or partially submerged objects. Cold temperatures are presumed to be the cause of annual die-offs of large numbers of shad in the waters of the Delta (Turner 1966a).

Threadfin shad are found usually east of Sherman Island, except during times of high outflow. Their catch in Bay Study trawls was remarkably constant and low (Table 7) for all years except 1983, which can be attributed to washout from upstream since that was the wettest year on record in California. Most of the catch occurred during the wet season of each year and, as the drought progressed through the last years of the study, threadfin shad were increasingly restricted to the wetter months.

Table 7. Sum of catch of threadfin shad in Bay Study hauls. Both nets and all stations combined. Forty-two percent of the catch was made in the midwater trawl at the four easternmost stations.

at the four subsequent years												
YEAR	MONTH											
	1	2	3	4	6	7	8	9	10	11	12	TOTAL
80	1				2			9	31	1		44
81						2				3	29	34
82	9	2	1				5		4	7	8	36
83	23	5			1		4	89	41	29	41	233
84	13	9		3				1	15	13	12	66
85	1	10	2						3	3	18	37
86	3								14	1	18	36
87	14	2	1							1	26	44
88	22	6					1				9	38
TOTAL	86	34	4	3	3	2	10	99	108	58	161	568

In the Fall Midwater Trawl surveys threadfin shad were the most abundant species of fish caught in the Delta for all but five years since the study began in 1967 (Table 8). The portion of the population of threadfin shad inhabiting the Sacramento River waters appears to be subject to somewhat different processes than those shad living in San Joaquin River waters.

Table 8. Abundance of five most abundant species in Delta in the catch of the Fall Midwater Trawl Survey. All stations east of Chipp's Island included.

Year	Striped Bass	Shad American	Shad Threadfin	Smelt Delta	Smelt Longfin	TOTAL FISH
67	2033	1423	8579	141	410	13014
68	2336	318	3403	429	127	6898
69	1097	1325	5161	62	177	8142
70	711	182	1428	122	10	2625
71	407	236	2120	252	44	3265
72	482	57	1913	136	11	2644
73	283	131	441	70	9	1358
75	281	419	326	48	22	1177
76	123	40	295	82	30	606
77	861	159	3717	468	162	5620
78	752	725	740	101	270	3041
80	645	1489	2865	594	1413	7069
81	754	302	2752	49	277	4220
82	402	1246	976	41	140	2834
83	180	447	526	1	13	1189
84	468	95	302	36	319	1280
85	397	310	448	68	307	1623
86	1741	592	1326	83	535	4443
87	663	341	1757	227	390	3541
88	205	789	1081	87	204	2411
TOTAL	14821	10626	40156	3097	4870	77000

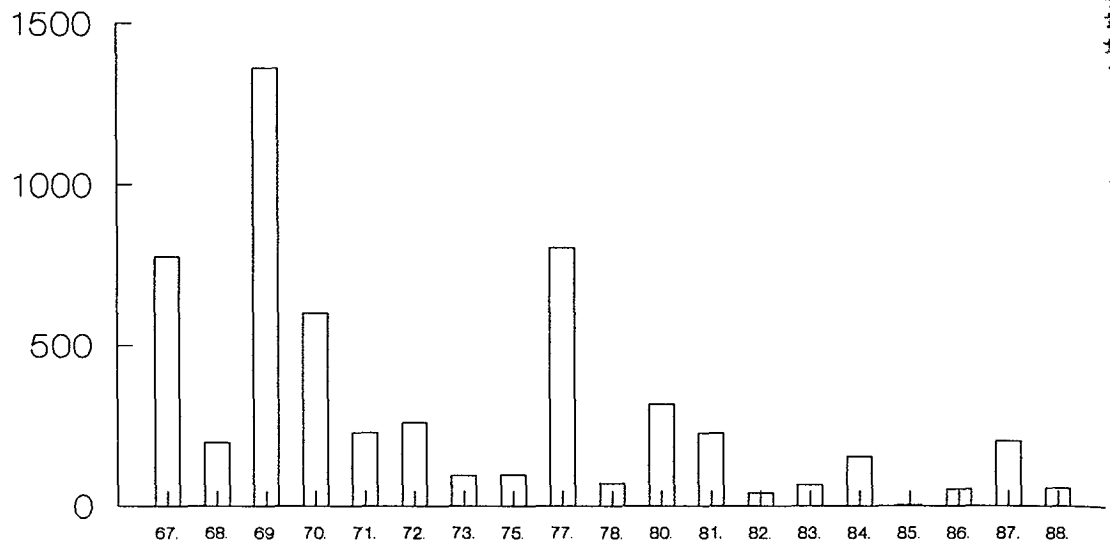


Figure 60. Catch of threadfin shad in September at stations consistently sampled by the Fall Midwater Trawl survey.

The greatest number of shad have been captured in San Joaquin River waters. Examining several representative years shows the spatial and temporal distribution of the species. In September almost all the shad are concentrated at the stations furthest upstream. After the onset of the rainy season shad begin to be captured at stations further downstream, so that by December threadfin shad are at their lowest numbers and greatest distribution. Die-offs of threadfin shad are a frequent occurrence in the lower estuary as temperatures drop to below the shads' lower tolerance level. Across years there is a declining trend of threadfin shad abundance at most stations, primarily due to exceptionally high catches in the first few years of the study which have not been seen since (Figure 60).

Embedded within the general decline in abundance are differences in the rate of decline at different stations. Four stations in the area with the greatest number of threadfin shad were sampled in September of all years. In October the water year begins and shad densities decline sharply at all stations as the shad are transported downstream. Data from these stations were analyzed to look for patterns in the association between the abundance of threadfin shad and the location of the station in the path of cross-Delta flows.

Two of these stations (910 and 912) are in the San Joaquin River near Stockton and receive only San Joaquin river water. The other two stations (906 and 908) are in the path of flow from the cross-Delta channel. All stations show a significant correlation with year. Diversion rates also increased across years so that a correlation with diversion is inevitable. In order to determine if being in the path of cross-Delta flow is tied to rapidity of shad decline, we examined partial correlations remaining after removing the effects of the correlation in both variables with year. Both stations in the path of diverted water showed

only significant partial correlations between September shad abundance with the quantity of water diverted during the preceding six months. The two stations upstream showed no significant partial correlations.

In the Sacramento River threadfin shad are much less abundant but they are more evenly dispersed than in the San Joaquin. Stations closer to the central Delta generally support the largest catches of threadfin shad. After the start of winter rains they are quickly displaced.

Adult threadfin shad are most abundant in the dead-end sloughs of the Delta and, so, are usually less susceptible to capture by the Fall Midwater Trawl series than are young-of-year. Data on fish lengths from this dataset are only available for the three years 1986-1988, however average lengths decreased significantly for each successive year of this period. This shrinkage of mean size is most likely the result of decreasing washout of adults from the dead-end sloughs because these three years were the beginning of a long period of little rainfall. Thus, more of the catch was probably younger fish coming from upstream populations and fewer from adults residing in the Delta. The effect of washout on the number of fish captured in the midwater trawls is shown by the downstream spread of threadfin shad over the course of the four months of the fall midwater trawl surveys.

4.7.11 Conclusions about planktivores

The planktivores of the Sacramento-San Joaquin estuary cover a wide variety of species with varying distributions and uses of the estuary. Eggs, larvae, juveniles, and adults of northern anchovy occur principally in the lower part of the estuary with a peak in abundance during the summer. Pacific herring adults only enter the Bay to spawn; the larvae feed in the Bay. Similarly, American shad adults migrate into the estuary to spawn, but they move through the Bay and spawn, mostly, upstream of the Delta. Adult longfin smelt live throughout the Bay, are seldom found outside the Bay, and migrate into the Delta to spawn. Delta smelt adults are found usually in Suisun Bay and the Delta and migrate into the Delta to spawn. Threadfin shad live in the Delta and upstream areas and are generally only found in the Bay complex as a result of high outflows in the fall and winter.

Expected trends for San Francisco Bay populations of northern anchovy and Pacific herring in the face of projected changes to the Bay include a continued dominance of the fish community by northern anchovy. This species is not limited to spawning only in the Bay and is not limited to any particular habitat in the Bay. Pacific herring appear potentially more sensitive to the effects of global warming. Increasing severity and frequency of winter storms may directly interfere with successful spawns by erosion of shallow habitats that support the algae they spawn upon, and by forcing conversion of these habitats into backwaters and dikes to protect low-lying property.

American shad are probably the anadromous species best able to survive the continuation of present conditions or of most foreseeable changes in estuarine habitat. Both adults and

juveniles pass through the estuary rapidly. By spawning in tributary rivers, American shad do not face the loss of spawning habitat that salmon have suffered. Their ability to spawn repeatedly also allows the population to survive years when spawning conditions are poor. They are also out of reach of entrainment by water diversions in the Delta that are the most likely cause of declines in the smelt and striped bass. The larger size of adult American shad makes them less susceptible to displacement by changes in flow patterns than either of the smelts or of threadfin shad.

Threadfin shad appear to be ill-suited to the present flow regime in the Delta because they are easily entrained and difficult to screen. However, upstream populations are large and can be expected to continue to provide large numbers of individuals to populate the Delta. Deepening of channels across the Delta and decreased transit times of water will serve to increase the displacement or entrainment of threadfin shad. Flooding Delta islands might provide the sorts of reservoir-like habitats where threadfin shad populations in the state have thrived. Alternative water transport plans are likely to most seriously affect the upstream reaches of the Delta and so amplify their current effects on threadfin shad.

The two smelt species do not overlap greatly in geography, habitat, or diet but they do spawn in the same area. Their parallel declines in abundance are most likely due to the changes in their spawning habitat. The recent switch to conditions of net reverse flow in their spawning grounds for most of their spawning seasons, which coincides with their rapid declines, provides a simple and sufficient explanation for their present plight. The dissimilarity of response to the dry year 1981 suggests that dry years, by themselves are insufficient to threaten the survival of the species.

Both smelts are likely to continue to suffer loss of young due to their requirement of breeding within the Delta, which will probably continue to be an inhospitable place during low flow years for any fish with planktonic larvae. Levee failures, however, could provide major increase in suitable habitats for feeding and maturation of Delta smelt. This species is likely to have been much more broadly distributed in the Delta prior to diking, dredging, and water diversion because more of the water would have probably supported zooplankton densities sufficient to support young smelt. The present restriction to the entrainment zone makes them more susceptible to displacement and entrainment than longfin smelt, but water storage on islands in the western Delta, or levee failures, might provide habitats similar to the original Delta in which they evolved.

4.7.12 White croaker

While much research and discussion has surrounded the biology of striped bass in the estuary, almost nothing has been written on the biology of the most abundant native piscivore in the Bay, white croaker (*Genyonemus lineatus*; Figure 61). White croaker eat a wide variety of foods including a number of small fish species. Although they generally live and feed near the bottom they have been observed chasing schools of northern anchovy at the surface (Love 1991). A partial explanation for the difference in intensity of scientific study is reflected in the attitudes of many Caucasian anglers who have a variety of unpalatable names for white croaker (e.g. 'sewer trout' [Love 1991]). However, they are avidly sought and eaten by anglers and shoppers of several ethnic minorities, and they are extremely abundant in the middens of coastal Indians of California (Love 1991).

White croaker, or kingfish, are similar to striped bass in several important respects. White croaker mature in 2-3 years and can live for up to 15 years (Frey 1971). Striped bass males mature in 1-3 years, the females mature in 2-4 years and can live up to 30 years (Raney 1952, 1954; Moyle 1976). Striped bass spawn April through June in the rivers and white croaker spawn from November to May, mostly in the Gulf of the Farallones. Eggs in both species are non-adhesive and pelagic. In both species currents play an important role in the distribution of larvae: river currents carry the newly hatched striped bass downstream to Suisun Bay and concentrate them in the entrapment zone, bottom or tidal currents carry newly hatched croaker into the Bay where they congregate in shallow areas. Juveniles of both species may move to the ocean as they mature but all life stages occur in the estuary.

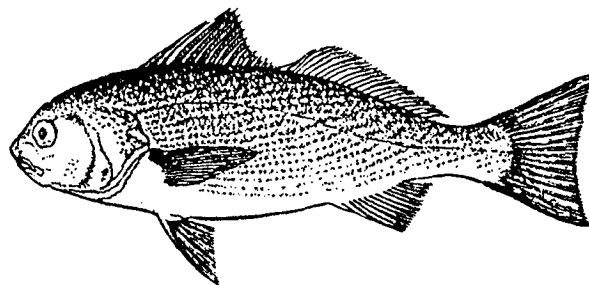


Figure 61 White croaker, adults to 40 cm (modified from Eschmeyer et al. 1983).

Significant ecological differences distinguish the two species: Striped bass spawn above or in the upper reaches of the estuary whereas white croaker spawn in the Gulf of the Farallones or in the lower reaches of the estuary. White croaker are primarily bottom fishes from the time they hatch and are quite omnivorous, but striped bass are dependent on neritic food at all stages of their life. Striped bass are much more euryhaline than croaker and, so, occur much more abundantly in the freshwater parts of the estuary.

The white croaker population in San Francisco Bay uses the Bay in three different ways, depending on age (Figure 62). Eggs are broadcast around April in the Central Bay or outside the Golden Gate and are carried by tidal currents into upstream parts of the Bay (Wang 1986). Young of year greater than 15 mm FL usually begin to be collected by the Bay-Delta study in May (Figure 63a). At about the same time juveniles from the preceding year's spawning re-enter the bay and concentrate in the deeper stations of South Bay (Figure

63b). The deeper stations of South Bay also support a year-round population of older fish (Figure 63c). In October or November the young of year and juveniles migrate out of the Bay. In recent years more adults have moved into shallow areas of San Pablo Bay during the spawning season, perhaps as a response to increasing salinity due to drought conditions. Thus, all three life stages migrate into the Bay but movements are in response to different conditions and are largely independent of each other.

Abundance of young-of-year white croaker shows little evidence of trends across the nine years of data. Catches in 1980, 1986, and 1988 were all at very similar high levels and more than twice that of most other years. These years of high catches do not appear to share any distinguishing features in their weather patterns. The abundance of young-of-year is uncorrelated with the abundance of juveniles in the following year or with the abundance of older fish two years following.

White croaker have changed in abundance, distribution, and age distribution in San Francisco Bay since the start of the Bay Study. Juvenile and adult croaker abundances in the Bay are both tightly correlated with the passage of time (Spearman's ρ for both = .97, $p < .01$). Adult croaker in the last years of the study were found more frequently in the shallow stations at the spawning season. Young of year white croaker are predominately found in the shoals of San Pablo Bay. The increasing use of the Bay as a spawning site probably explains the greater abundance of young of year in 1986 and 1988. Rank abundance of young of year is significantly correlated with the rank abundance of adults present in that year (Spearman's ρ = .67; p = .05).

Distribution of white croaker within the Bay presents a confused picture (Figure 64) because of the differing shifts shown by different age classes. Because fewer young appear to have entered the Bay in the recent years of low outflow, the abundance of young in San Pablo Bay has declined. However, the larger, more resident population of mature white croaker are spawning within the Bay so that young present in the Bay in recent years arise from an entirely separate process than the young caught in the earlier years.

Overall, it appears that the abundance of young in the Bay increases in response to greater immigration during high outflow years or in years when adults spawn in the Bay. However, in either case, the migration of young out of the Bay mixes them with a larger population in the ocean so that higher spawning in the Bay does not lead to higher catches in later years of juveniles or adults in the Bay.

White croaker appear likely to continue their spread of juveniles and adults into parts of the Bay previously only used by young-of-year, as salinities in those areas decline in variability. Increased water diversion rates in the face of increasing frequency of drought conditions and rising sea levels will both tend to stabilize salinities in San Pablo Bay, probably favoring fish like adult white croaker, which have been common in South Bay. Increased spawning within the Bay and decreased wintertime flows out of the Bay are likely to broaden the seasons when white croaker occur.

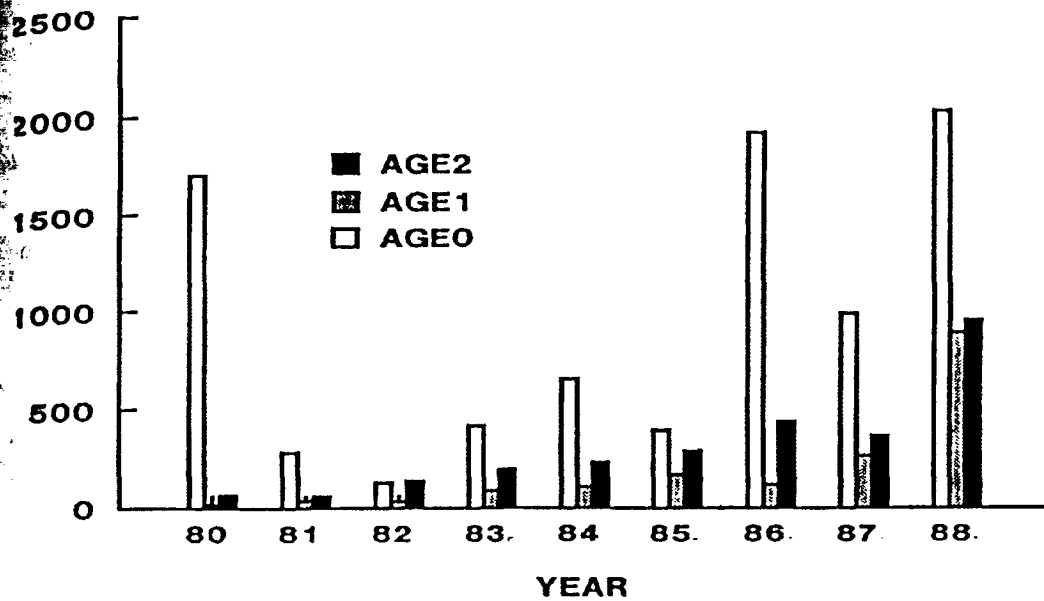


Figure 62 Presence of different life stages in San Francisco Bay through time of white croaker, from catches by the Bay study.

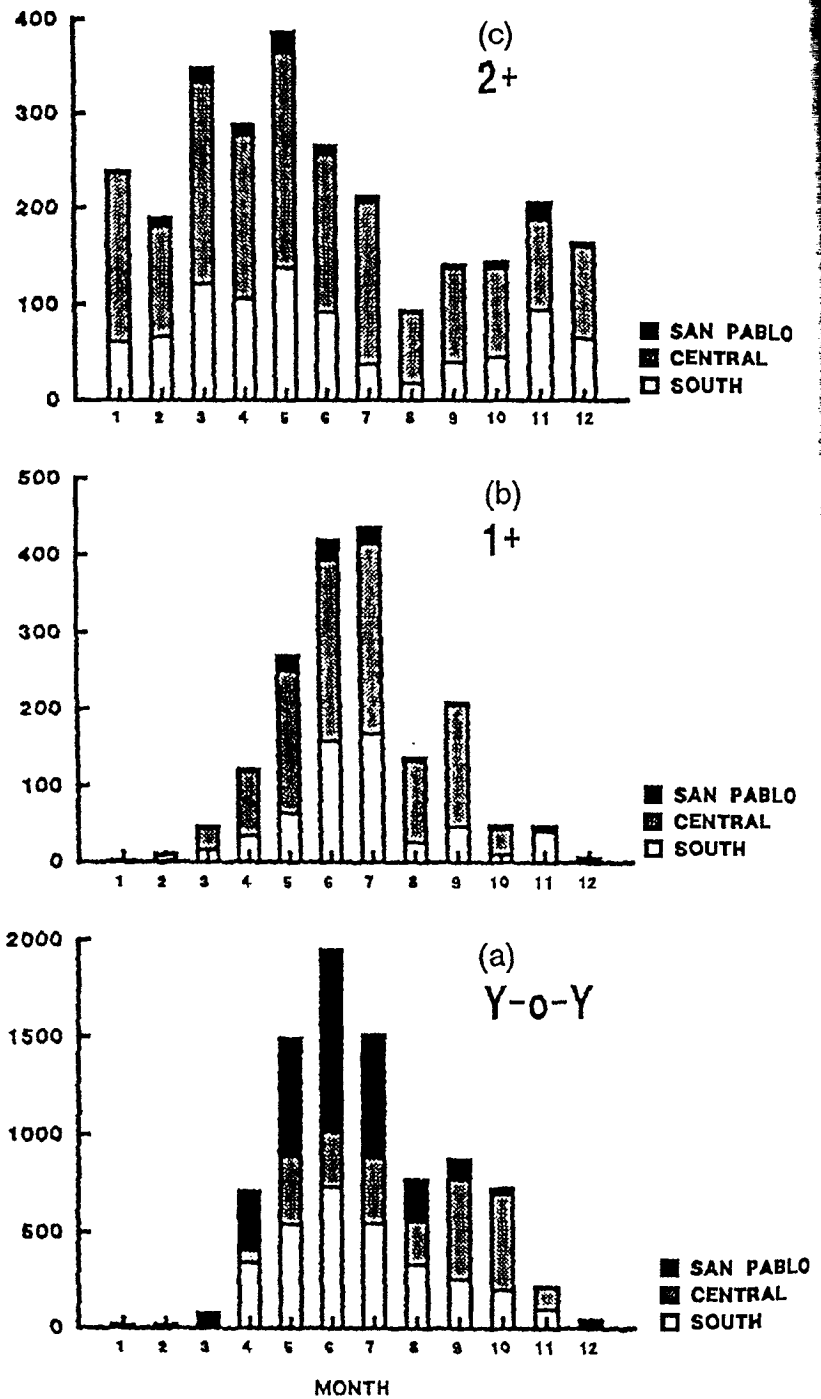


Figure 63 Abundance of three age classes of white croaker from otter trawls of the Bay study: the bottom is the catch of young of year, in the middle is of year old juveniles, at the top is data for two year old and older.

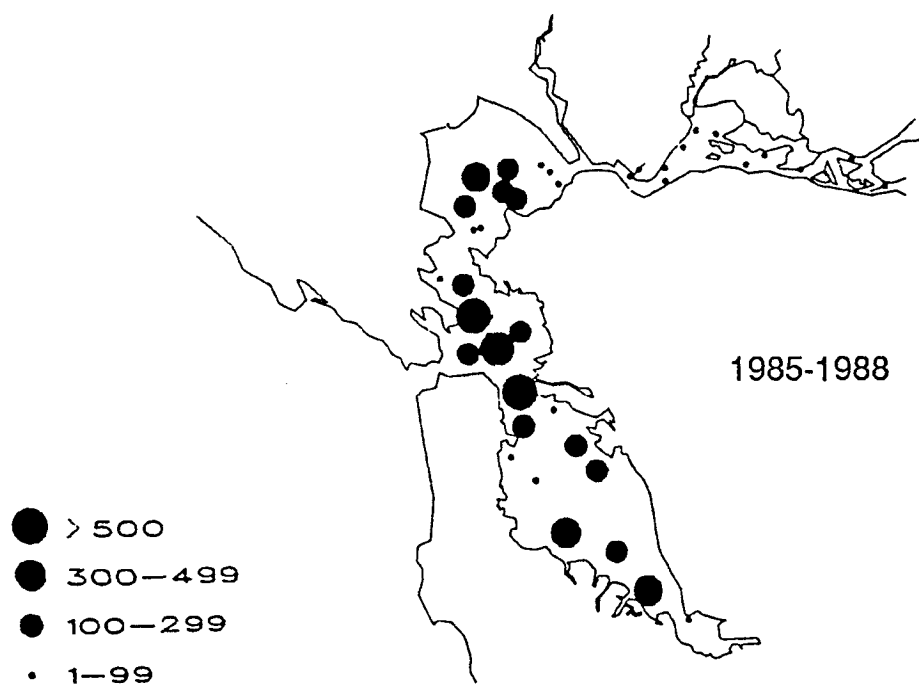
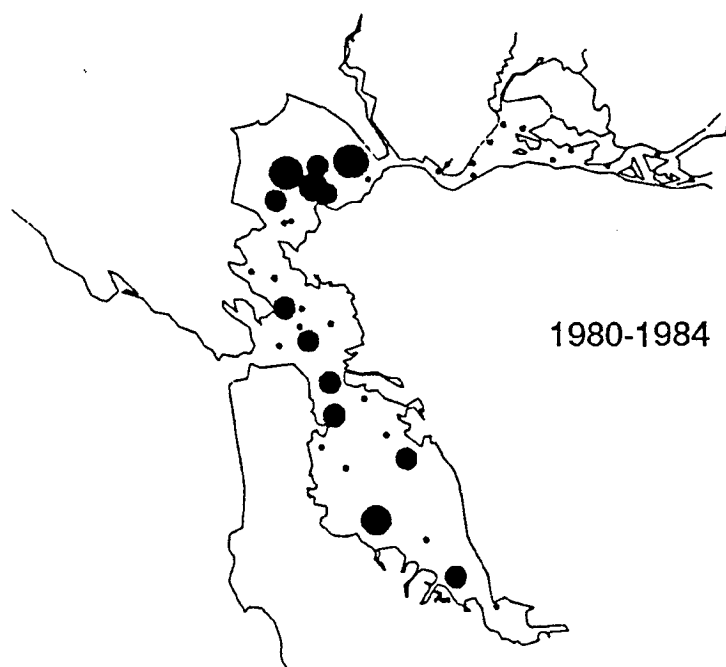


Figure 64 Distribution of all ages of white croaker for the first and second halves of the period of sampling by the Bay study

4.7.13 Flatfish

English sole (*Parophrys vetulus*; Figure 65) and starry flounder (*Platichthys stellatus*; Figure 66) are similar bottom-foraging flatfish that spawn outside the Golden Gate and immigrate into the Bay using a combination of density and tidal currents (Wang 1986; Lassuy 1989). Starry flounder penetrate much further into the Bay than English sole and can be found in the estuary throughout the year whereas English sole are markedly seasonal in occurrence (CDF&G 1987a).

English sole occur in the Bay predominantly as young of year. Adults support a commercial ocean fishery but do not enter the Bay in significant numbers. Spawning occurs in shallow areas all along the coast from November to May (Wang 1986). While newly released eggs are buoyant, they lose buoyancy immediately before hatching; however, newly hatched larvae are found at the surface. (Budd 1940). Larvae remain pelagic for 6 to 10 weeks (Ketchen 1956; Wang 1986). As the larvae transform, at a length of about 15-20 mm, they descend the water column and many are transported by currents into the Bay. The importance of San Francisco Bay as a nursery ground for the coastal population of English sole is uncertain but much of the Oregon population of adult English sole is the result of young raised in estuarine nurseries (Olson and Pratt 1973).

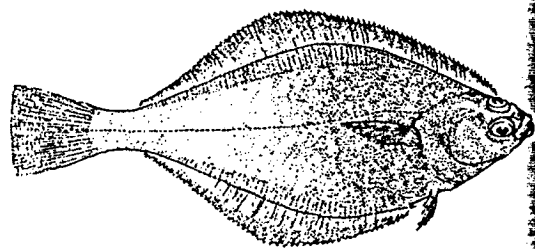


Figure 65 English sole, juveniles in Bay usually less than 12 cm (from Hart 1973).

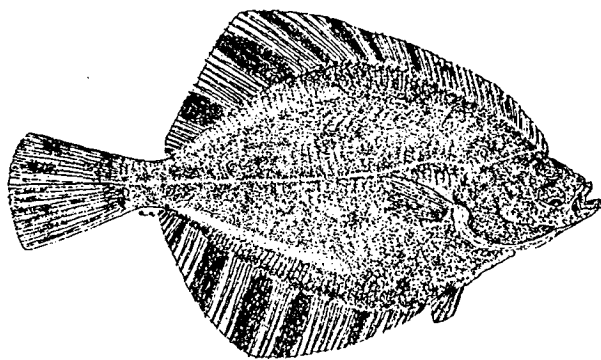


Figure 66 Starry flounder, juveniles usually less than 12 cm, adults to 90 cm (from Eschmeyer et al. 1983).

Starry flounder occur in San Francisco Bay in high numbers for all life stages. A substantial ocean population supports a small commercial fishery (Frey 1971), and adults in the Bay support a popular sport fishery. Early descriptions found larvae in the lower San Joaquin River and supposed that they were the products of adults spawning there and in Suisun Bay (Radtko 1966b). Later investigations have suggested that spawning takes place at the mouths of estuaries and bottom currents move the larvae inland (Wang 1986).

English sole and starry flounder both use bottom currents to transport their young into the Bay, but it appears that the Bay is more important as a nursery ground for starry flounder because their spawning adults appear more likely to migrate into the reach of bottom currents (Gunter 1942; Orcutt 1950).

English sole are more abundant than starry flounder in the catches of the Bay study, partly due to a much larger percentage of young of year. The English sole population in the Bay study otter trawls is almost exclusively young of year. New young of year appear in January, while the previous year's young are still present. By May the previous year's young (120-180 mm FL) have left the estuary and only the current season's young (20-100 mm FL) remain. They appear to greatly slow their growth in October.

Examination of length frequency histograms shows that starry flounder maintain at least three age classes throughout the year in both San Pablo and Suisun bays. The high abundance of young of year can temporarily mask the abundance of older fish in June-August, but by December the older fish comprise about half the catch. The smallest starry flounders are found further upstream in Suisun Bay from May to October. By November the modal size of young is the same in both bays. It seems most likely that the larger larvae settle out of the currents earlier than the smaller ones so that the young ones are transported further inland.

As with most other similar species in the estuary, the two abundant flounders have different centers of distribution (Figure 67). English sole are primarily in Central Bay and spill almost equally into South and San Pablo bays. Starry flounder are most abundant, and most diverse in sizes, in San Pablo Bay, but many young are found in Suisun Bay.

English sole have varied in catch at the Bay Study stations from a low of 417 in 1987 to a high of 2315 in 1984, but they show little evidence of a trend through time (Figure 68). English sole are most variable in their catch in San Pablo Bay; the highest catch in San Pablo Bay occurred in 1988 and constituted 60% of the total catch, but in 1983 San Pablo Bay accounted for only 5% of the catch.

Starry flounder show a pronounced trend through time (Figure 69). A sharp decline is apparent in the starry flounder catch since 1983; the last four years of the study are the four years of lowest flounder abundance. The decline has been sharpest in San Pablo Bay, which from 1985 to 1988 yielded less than 10% of the starry flounder captured at the same stations in 1980 to 1984. The decline in Suisun Bay is slightly less precipitous and principally reflects a reduced production of young (Figure 70). The concentrations of toxic PCBs in adult starry flounder have been shown to be sufficient to reduce reproductive success (Spies et al. 1988; Spies et al. 1990; Davis et al. 1991).

Examination of the spatial distribution of starry flounder emphasizes the two areas of concentration within the Bay (Figure 71). Near Alcatraz, the catch has declined but is still geographically isolated from the catch in San Pablo Bay. The population in San Pablo Bay

has drastically declined, and there is a corresponding decline in the number of young found in Suisun Bay. There may be two populations, an offshore one whose young appear near the mouth of the Bay and a resident one which appears to breed and stay year-round in the northern reaches of the Bay. If so, each population would be susceptible to different limiting factors.

English sole shows little or no evidence of decline in abundance in the Bay, despite the fact that almost all English sole in the Bay are young of year. English sole have spread further upstream in the recent drought years, and the largest catch (still only 10 fish) of English sole in Suisun Bay occurred in 1988. Starry flounder have declined, with greater declines in San Pablo Bay than in Suisun Bay.

The increase in English sole immigration and the decline of starry flounder in Suisun Bay suggest that the adult starry flounder in San Pablo Bay were affected by some extrinsic factor that was not acting on young English sole or on young starry flounder in Central Bay. Organic contaminants in San Pablo Bay have been shown to be sufficient to reduce the reproductive success of starry flounder (Spies et al. 1989, 1990).

The two flatfish species offer strong contrasts in expected trends in response to changing climatic conditions and benthic communities. The resident population of starry flounder appears to share the fates of striped bass, Delta smelt, and longfin smelt due to its dependence on hydrologic and other environmental conditions of San Pablo and Suisun bays. The future of starry flounders in the Bay appears to be that they will cease to maintain a separate inland population and will, like the English sole, only use the Bay for a brief period as a nursery area for young of year. The decline of the San Pablo Bay starry flounder population coincides with increased presence of English sole. This may reflect biotic interactions or simply greater dispersion due to increasing abundance of English sole young entering the bay. Bottom-dwelling habits, feeding on the benthos, and wide salinity tolerances may allow young flatfish of both species to continue using the Bay despite most projected changes in physical conditions.

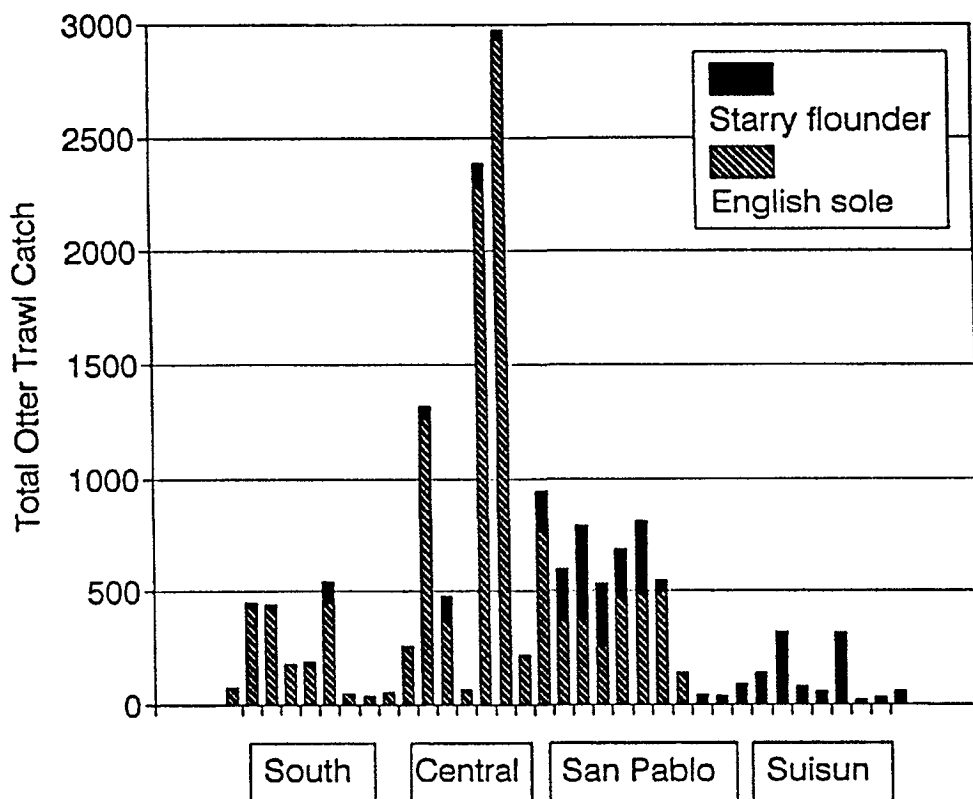


Figure 67 Distribution of abundance of English sole and starry flounder in otter trawls of the Bay study

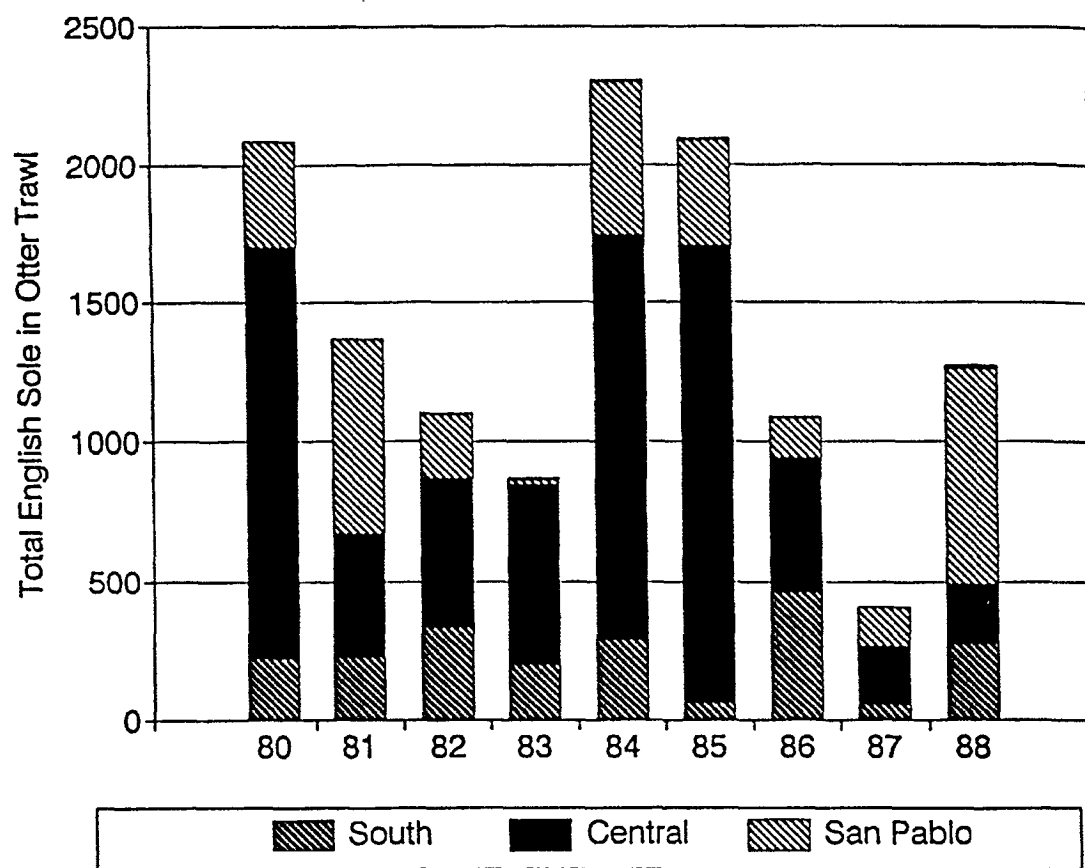


Figure 68 Catch of English sole through time, 1980-1988 (data from otter trawls of the Bay study).

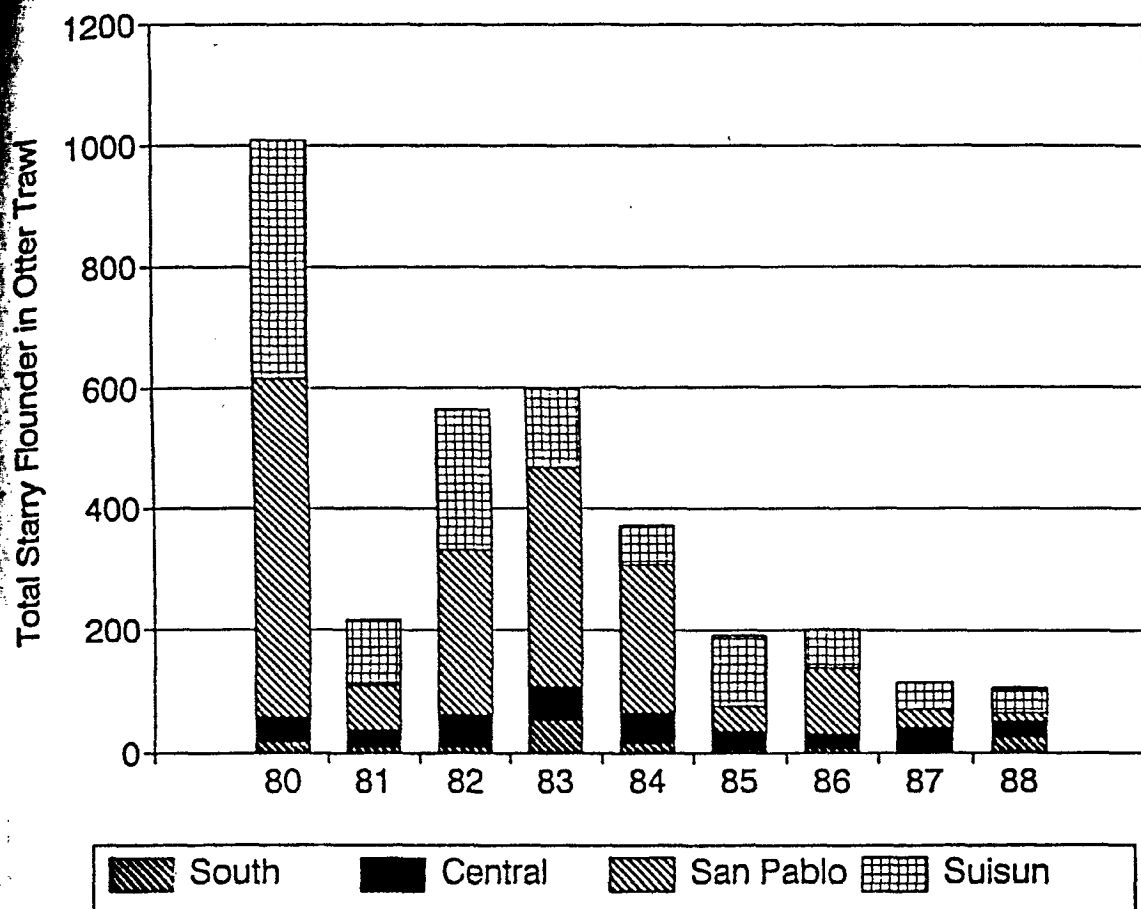


Figure 69 Catch of starry flounder through time, 1980-1988 (data from otter trawls of the Bay study)

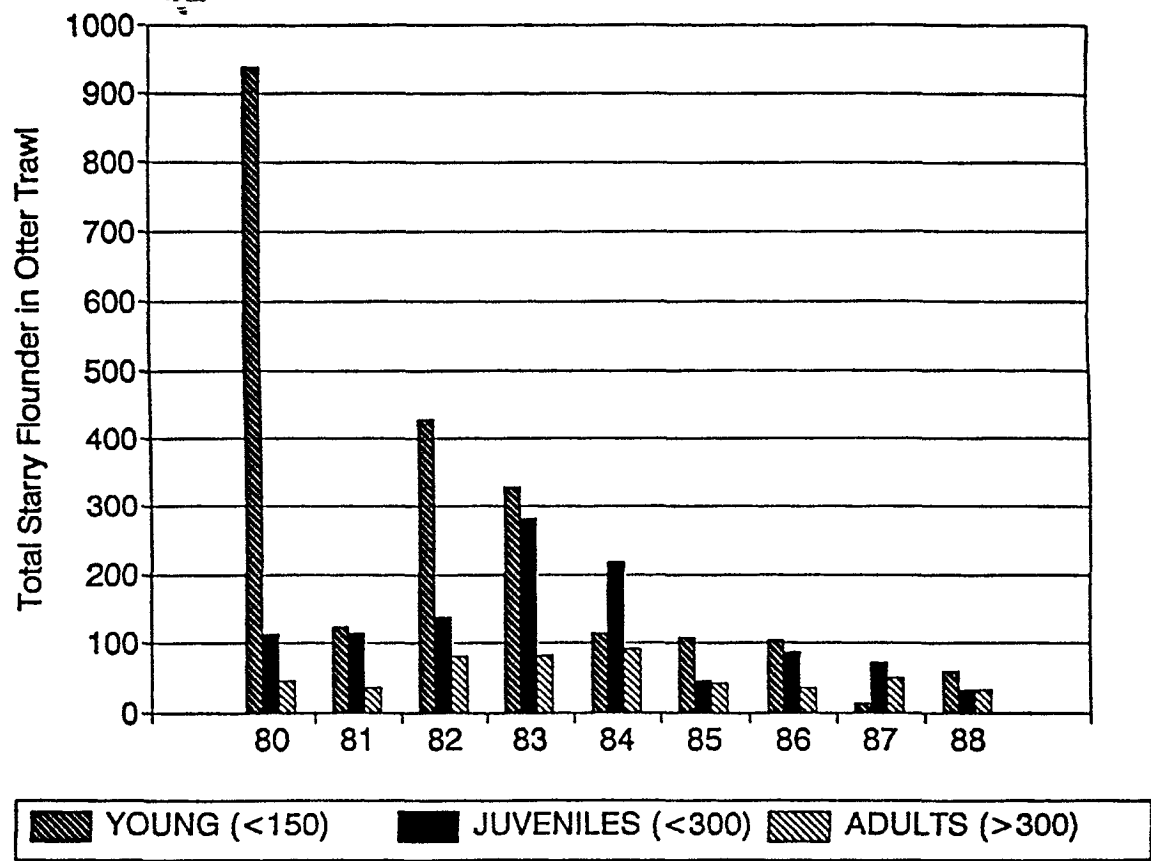
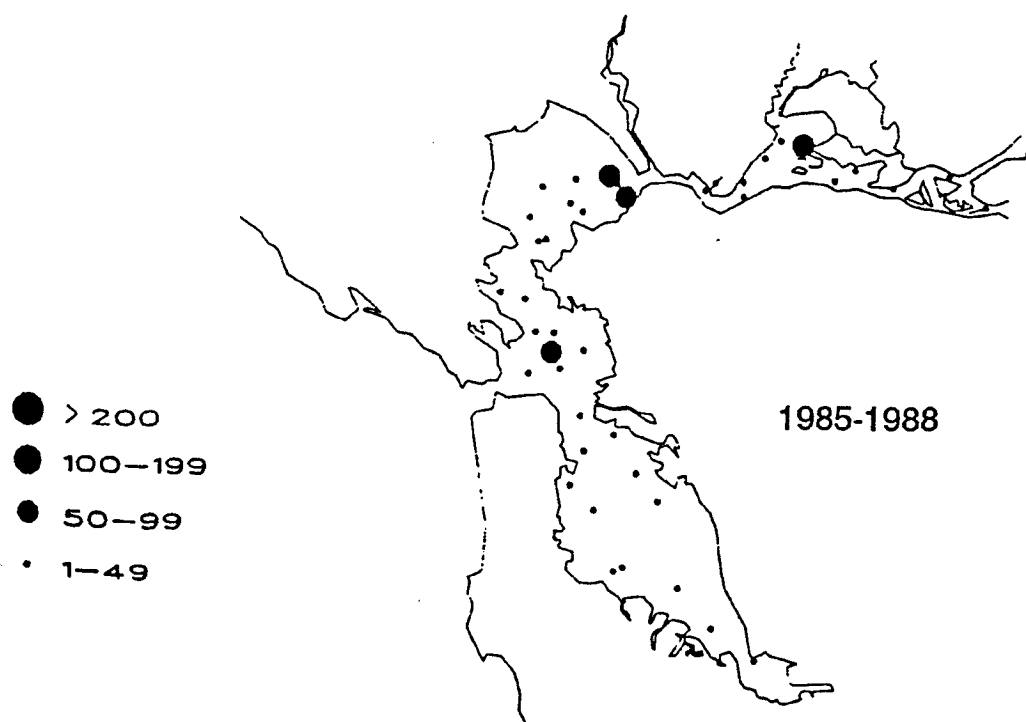
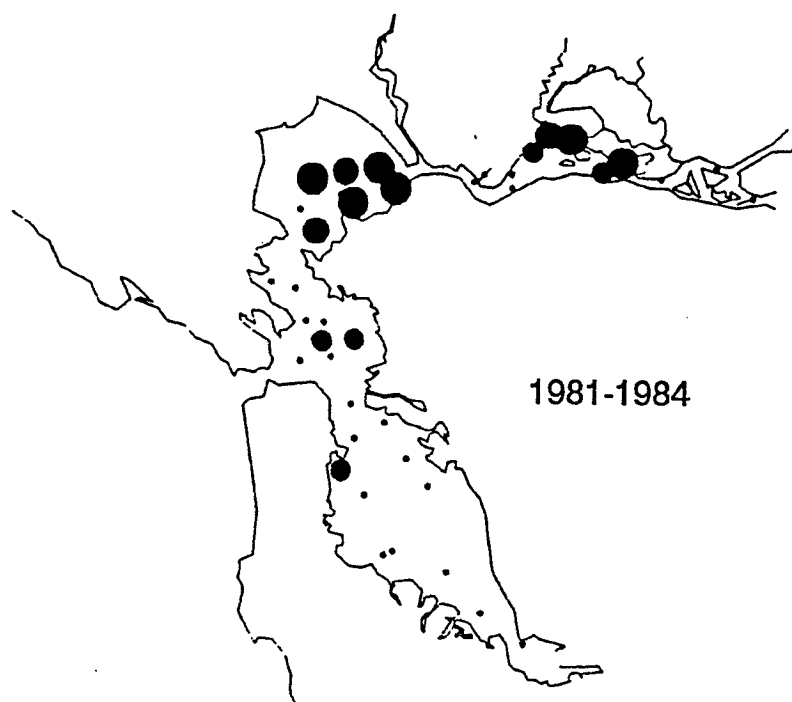


Figure 70 Trends across years of three age classes of starry flounder.



- > 200
- 100-199
- 50-99
- 1-49

Figure 71 Comparison of distribution of starry flounder between 1980-1984 vs 1985-1988.

4.7.14 Surfperches

Nineteen species of surfperch (family Embiotocidae; Figure 72) occur in California's waters; thirteen of them have been collected by the Bay Study. These fish are small live-bearers; the largest species seldom exceeds 18 inches and most are mature at only six to seven inches (Miller and Lea 1972; Eschmeyer et al. 1983). As their common name implies surfperches are most frequently found in the

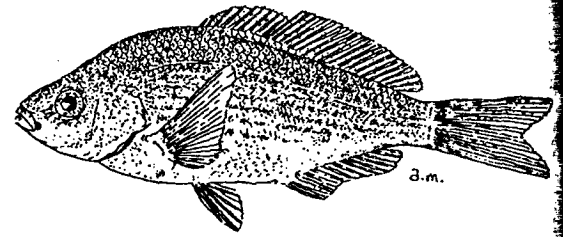


Figure 72 Shiner perch, adults to 18 cm.
(from Moyle 1976)

surf zone, both over sandy beaches and in rocky areas. Studies of their behavior in kelp forests and rocky reefs show that they are usually rather sedentary, with the same individual often being found in one area for long periods of time (Hixon 1980; Ebeling et al. 1980). All species give birth to fully developed young which immediately begin feeding in the same habitat and manner as the parent. Most species are primarily found in marine habitats but the shiner perch (*Cymatogaster aggregata*) is usually found in bays, and is more than ten times as abundant as any other member of the family in the catches of the Bay Study. California is the only home of the only freshwater member of the family, the tule perch (*Hysterocarpus traski*). Tule perch are patchily distributed throughout the Sacramento Valley, with a large population in Suisun Marsh. Because they feed among emergent vegetation, tule perch are not captured often by either the Bay Study or the Fall Midwater trawl survey; however the sampling program in Suisun Marsh of University of California at Davis collects them frequently. The species that occur in the Bay but have most of their populations along the coast, may be transported into the Bay by bottom currents since they are bottom feeders that do not appear to travel great distances. However, some species have been shown to migrate in response to changes in ocean temperature or toward warm water from power plant discharges (Allen et al. 1970; Terry and Stephens 1976; Hose et al. 1983). The species in the Bay include black surfperch (*Embiotoca jacksoni*), white surfperch (*Phanerodon furcatus*), pile perch (*Rhacochilus vacca*), dwarf surfperch (*Micrometrus minimus*), and barred surfperch (*Amphistichus argenteus*).

Because they are live-bearers, surfperch reproduction is not apt to be affected by the sort of changes in habitat or food abundance that are likely to affect the larvae of most other fish.

The surfperches of San Francisco Bay can be placed into three groups:

- 1) the freshwater tule perch,
- 2) the euryhaline shiner perch, which is characteristic of the Bay below Carquinez Strait, and
- 3) marine species.

These three groups show two patterns of abundance through time in the Bay. The marine species have all declined in the catch of the Bay Study since the mid-1980s. Prior to 1985 the species show few similarities in patterns of abundance (Figure 73). However, all species

to lower levels in the period 1983-84, and since then the less abundant species have remained at lower abundances. This cannot be entirely ascribed to weaker bottom currents because there is no consistent pattern in any of the species with earlier patterns of outflow.

Tule perch and shiner perch, although they show very little overlap in geographical distribution, show very similar trends in abundance through time (Figure 74 and Figure 75). Both species declined in 1983, a year of extremely high outflow, and gradually recovered over the following four years. The decline in shiner perch is greatest in San Pablo Bay and least in South Bay. The mechanism producing this decline is unclear but the timing and area of greatest effect indicate that the very high outflow of this year is involved. Perhaps some other aspect of *El Niño*, which produced the high outflow, might be responsible for the decline, but the more marine surfperch show no apparent change in abundance from 1982 to 1983.

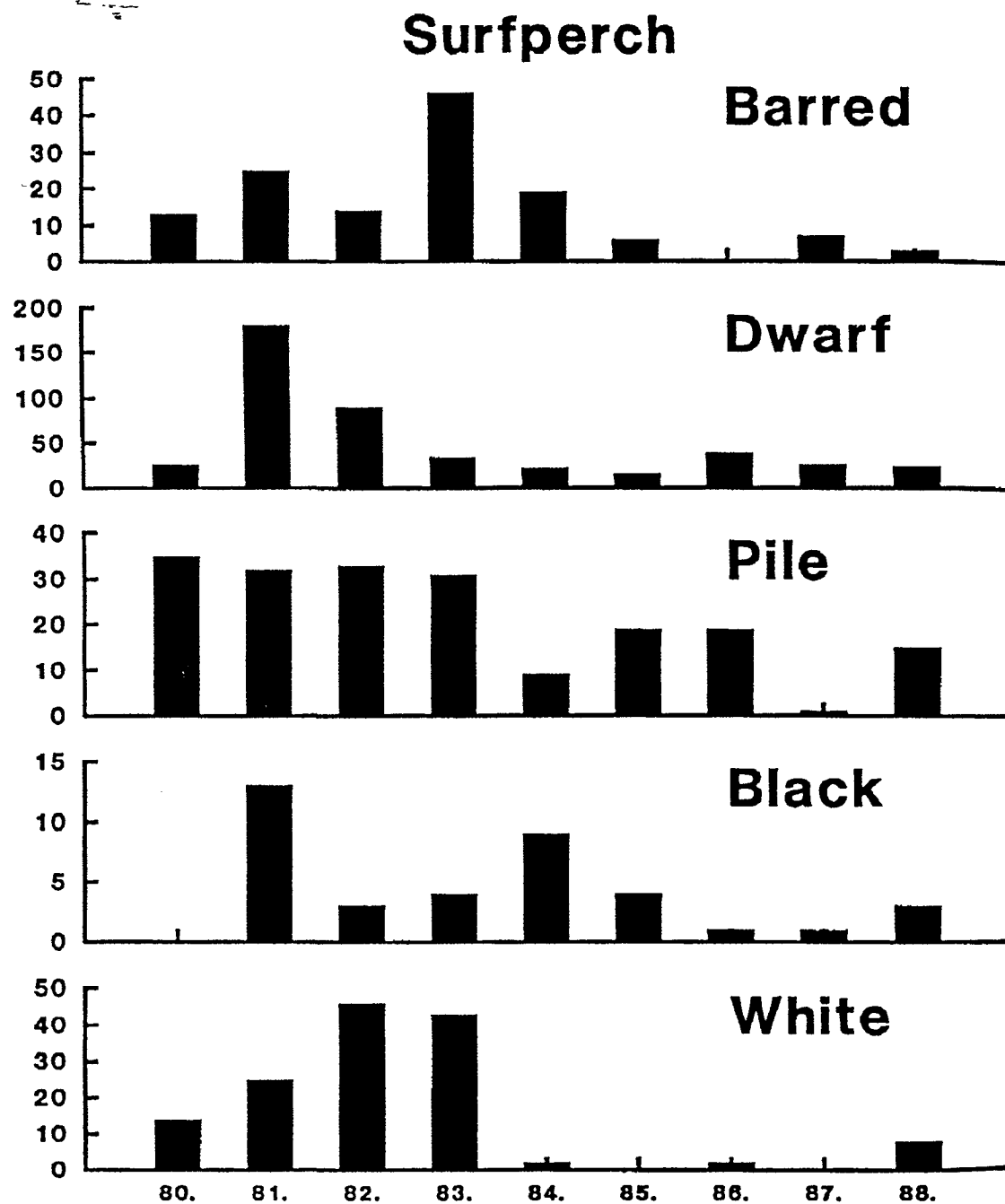


Figure 73. Catch of five marine species of surfperches through time from data of the B& Study.

Shiner Perch

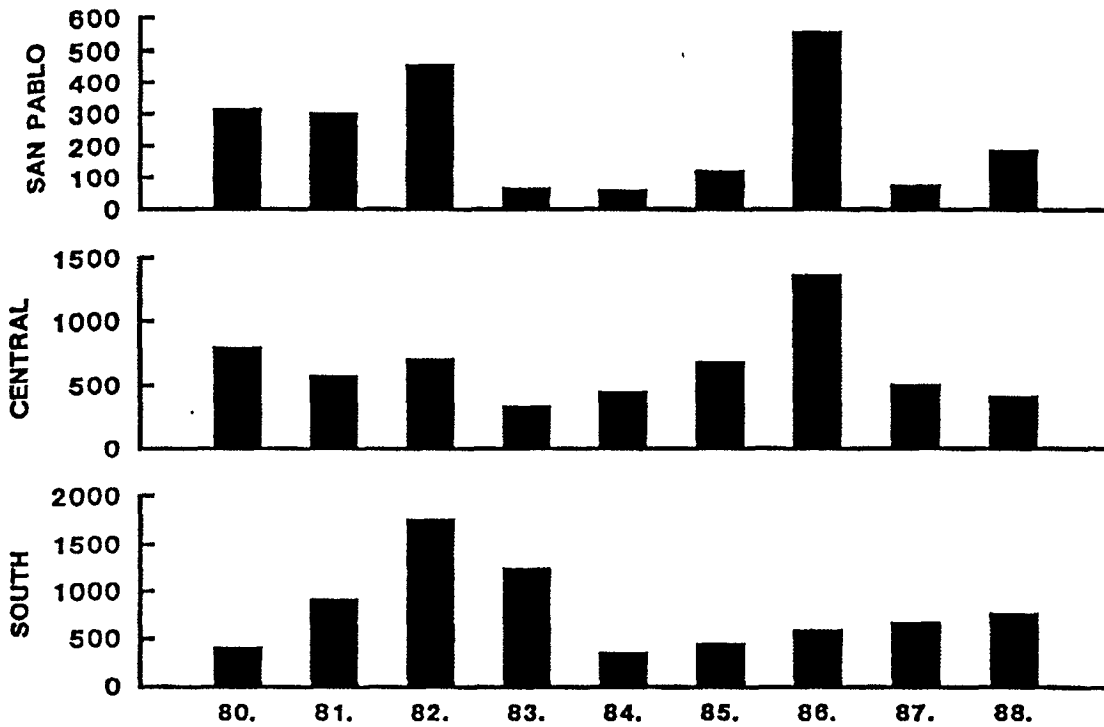


Figure 74. Catch across years of shiner perch in otter trawls of the Bay Study in each of the lower embayments.

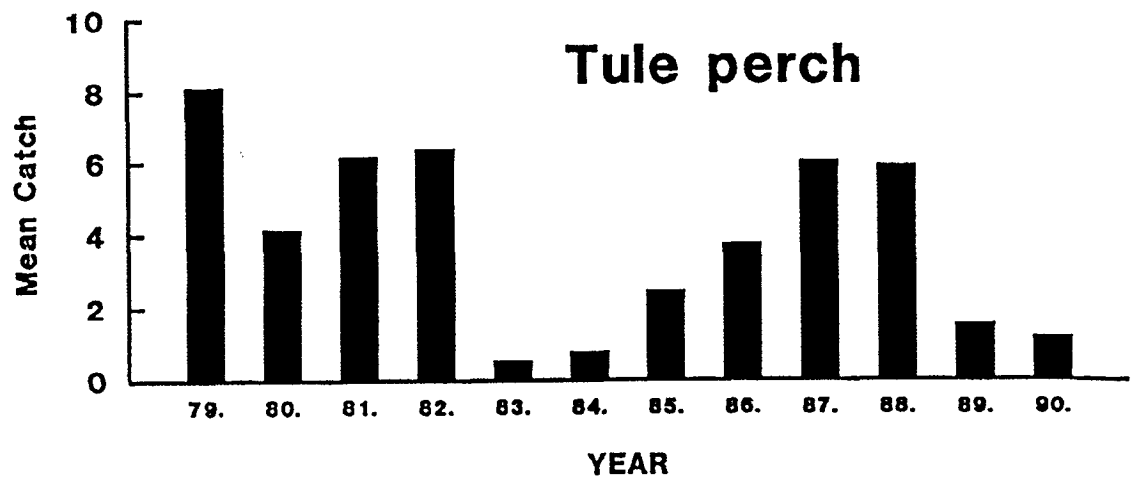


Figure 75. Catch per trawl of tule perch in otter trawls performed in Suisun Marsh by UCD personnel.

4.7.15 Native freshwater fishes

Data is largely lacking on the trends in the abundances of other native freshwater fishes in the Estuary, but some general comments are nevertheless possible. Sacramento squawfish (*Ptychocheilus grandis*), Sacramento sucker (*Catostomus occidentalis*), and Sacramento blackfish (*Orthodon microlepidotus*) are still fairly common. Squawfish and sucker are most abundant in the western Delta where water quality is highest, but can be found throughout the upper estuary, while blackfish are largely confined to dead-end sloughs (Turner and Kelley 1966; CDFG, unpublished data). Hitch (*Lavinia exilicauda*) are also characteristic of dead-end sloughs, but they are generally less abundant and more scattered in their distribution than blackfish; their status in the Delta is uncertain.

Sacramento splittail (*Pogonichthys macrolepidotus*) were once found throughout the Central Valley but are now confined to the Estuary (Moyle 1976). Their reproductive success is positively correlated with outflow (Daniels and Moyle 1983). In Suisun Marsh, they have declined steadily in abundance since 1979 (Moyle et al. 1985; Herbold and Moyle, unpublished data), a trend which is probably characteristic of its populations in the entire estuary. Thicktail chub (*Gila crassicauda*) and Sacramento perch (*Archoplites interruptus*) are now extinct in the Estuary (the chub is globally extinct), although both species were formerly abundant enough to be heavily utilized by local Native Americans (Schulz and Simons 1973). Sacramento perch were also harvested commercially in the 19th Century (Skinner 1962). The last thicktail chub was collected in the Delta in 1957, but the Sacramento perch is abundant in alkaline reservoirs and lakes into which it has been introduced, outside its native range.

5 Aquatic Habitats and Communities of the Estuary

5.1 Tributary streams

Most studies of aquatic resources have focussed on processes and species that occur within arbitrary boundaries that divide the estuary from the surrounding land. Runoff as a contribution to non-point sources of pollution has been recognized as one interconnection between the numerous small streams of the bay area and the bay itself. Appendix A describes the importance of outflow from such streams as contributions to the carbon budget of different parts of the bay. However, the role of these streams as repositories of aquatic resources of the bay has received little attention in recent years.

There are approximately 175 tributary streams in the Bay area with approximately 60 creeks that flow directly into the Bay. Most streams have suffered, especially in their lower reaches, from habitat loss through channelization, removal of riparian vegetation, reduced water quality, and the construction of barriers to fish migration (Leidy 1984). Some still support runs of steelhead (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and chinook salmon (*O. tshawytscha*).

The abundance of native fish species in these streams generally reflects the intensity of urbanization of the surrounding lands (Aceituno et al. 1973; Scoppettone and Smith 1978; Leidy 1984; Leidy and Fiedler 1985). Leidy (1984) examined the distribution and abundance of fishes in these creeks in 1981. In North Bay streams, native species were dominant in 76% of the sampled sites and only 10% of the sampled sites were fishless. In streams of the east side of the Bay and north of Alameda Creek, 60% of the sites were dominated by native species. In South Bay streams only 42% of the sites were dominated by native fishes and 30% of the sample sites were fishless.

The fishes of the tributary streams of the Bay Area are particularly sensitive to habitat loss. Resident freshwater populations are isolated from each other by the salt water of the Bay. Hence, many of the native species are incapable of recolonizing a stream that loses its native fauna. The drought of 1976-1977 was suspected to be responsible for the disappearance of at least one native fish (hardhead, *Mylopharodon conocephalus*) that had been recorded from Bay Area streams previously (Leidy 1984). The mouths of these creeks also provide numerous examples of estuarine conditions that are favored by some taxa. The Newwater goby (*Eucyclogobius newberryi*) is a species listed by the State Department of Fish and Game as threatened and was formerly found at the mouths of 10 of the 60 creeks flowing into the Bay; they are now extirpated from at least 9 of their former Bay locales (Moyle et al. 1989).

5.2 Salt ponds

Large areas of what was formerly tidal marsh habitat near South and San Pablo bays have been transformed into salt ponds. Around San Pablo Bay these ponds comprise 36 km²;

South Bay salt ponds are about three times as extensive (111 km²; Lonzarich 1989). These ponds increase in salinity as the water evaporates, and consequently they harbor different arrays of species at different 'ages' of the ponds. As the ponds fill, several species of shallow habitats are commonly found, including topmelt, threespine stickleback, longjaw mudsucker, staghorn sculpin, and rainwater killifish. At higher salinities the species list shortens until only topmelt are left in the ponds of South Bay (Carpelan 1957) and threespine sticklebacks in the ponds near Napa.

The invertebrate fauna of these ponds shows a similar reduction in diversity through time. Recently filled ponds support dense populations of several worms, clams, snails, benthic crustaceans, and insects (Carpelan 1957; Lonzarich 1989). At the highest salinities only brine shrimp (*Artemia salina*), water boatmen (*Trichocorixa reticulata*), and water striders (*Ephydra millbrae*) are found.

These ponds are very important habitat for a number of waterfowl species (Harvey et al. 1988), but their aquatic populations are isolated from the other aquatic resources of the Bay. The status and trends of salt pond populations are, therefore, more thoroughly considered in the status and trend reports on wetland communities and on wildlife.

5.3 Fish distribution patterns

The Aquatic Habitat Institute has developed a segmentation scheme for the Sacramento-San Joaquin Estuary to reflect regions with distinct hydrodynamic characteristics. This segmentation scheme is designed to be particularly useful for tracking the effective areas of sewage outfalls and other physically dispersing materials (Gunther 1987). Unfortunately, the only sampling program with stations that are numerous and widespread enough to permit comparison with the AHI segmentation scheme is the CDF&G Bay Study (Figure 76). Thus, phytoplankton, benthos, epibenthos, and zooplankton can only be described, if at all, in broad geographical units, as in the preceding section. The degree to which the segmentation scheme corresponds to the distribution of fish is discussed below.

In this section we describe the distribution of fish species in the Estuary (exclusive of the upper Delta, for which little distributional data exists) to show how fish distributions are affected by season and by many of the physical features associated with hydrodynamics. Data are from the Interagency Ecological Program/San Francisco Bay Study (hereafter 'Bay Study'). This program has sampled with a variety of gear on a monthly basis throughout the Bay from January 1980 to the present. For this analysis we use the data through December 1988 for the 35 stations that were sampled on all sampling periods. We make no effort to analyze the distribution of species in relation to the measured salinity or temperature at each station for the Bay Study. These data are being analyzed by CDF&G and should appear shortly. We rely on the distance from the Golden Gate as a rough estimate of the mean salinity at each station and separate the data into quarterly groups to compare the degree to which species vary in their occurrence at a site in response to seasonal variability. Salinity

river outflow, and temperature doubtless affect the distribution of fish in the Bay but the purpose of this section is to identify those fishes that are most often found at each site.

The most abundant species in the midwater and otter trawls at each station for each quarter in the sampling of the Bay Study are described in Appendix B. Stations are identified by their place in the segmentation scheme of Gunther (1987). The species which were caught in more than one-third of the trawls made at a station are included, up to six, to give a profile of the types of fishes found in an area. The total number of species (spp.) is reported as an estimate of species richness. The total catch (catch) for the station over all nine years for all species in each quarter is given as an estimate of relative fish abundance in each quarter (these data can only provide a very rough estimate of fish abundance across stations because the efficiency of the sampling gear varies with depth, substrate, etc.). Because northern anchovy comprise about 80% of the fishes in the Bay the total catch is given for all species except anchovy and also the total with anchovy.

Analyzing the distribution of fish within each embayment to determine areas lacking common species can be as informative as noting the presence of species. Presence in one third of the trawls performed at each station over the nine years may under-represent rarer or less easily caught species. No replicate trawls were performed to examine consistency of catch within one station at one time. These biases make the descriptions of the species characteristic of each site and season conservative in that other species may also occur consistently but are sampled less efficiently or consistently. Comparison of the total number of species to the number that occur in each table in Appendix B gives a simple estimate of the predictability of catch at each site.

We attempt to describe the status of fishes by looking at the consistency of their distribution in space and by season. Species included in a table were present for all months of a quarter for all years, or were present in all months of the quarter for only three of the nine years of sampling, or were caught in only one month of the quarter but in each of the nine years. The description of trends through time is examined in a later section.

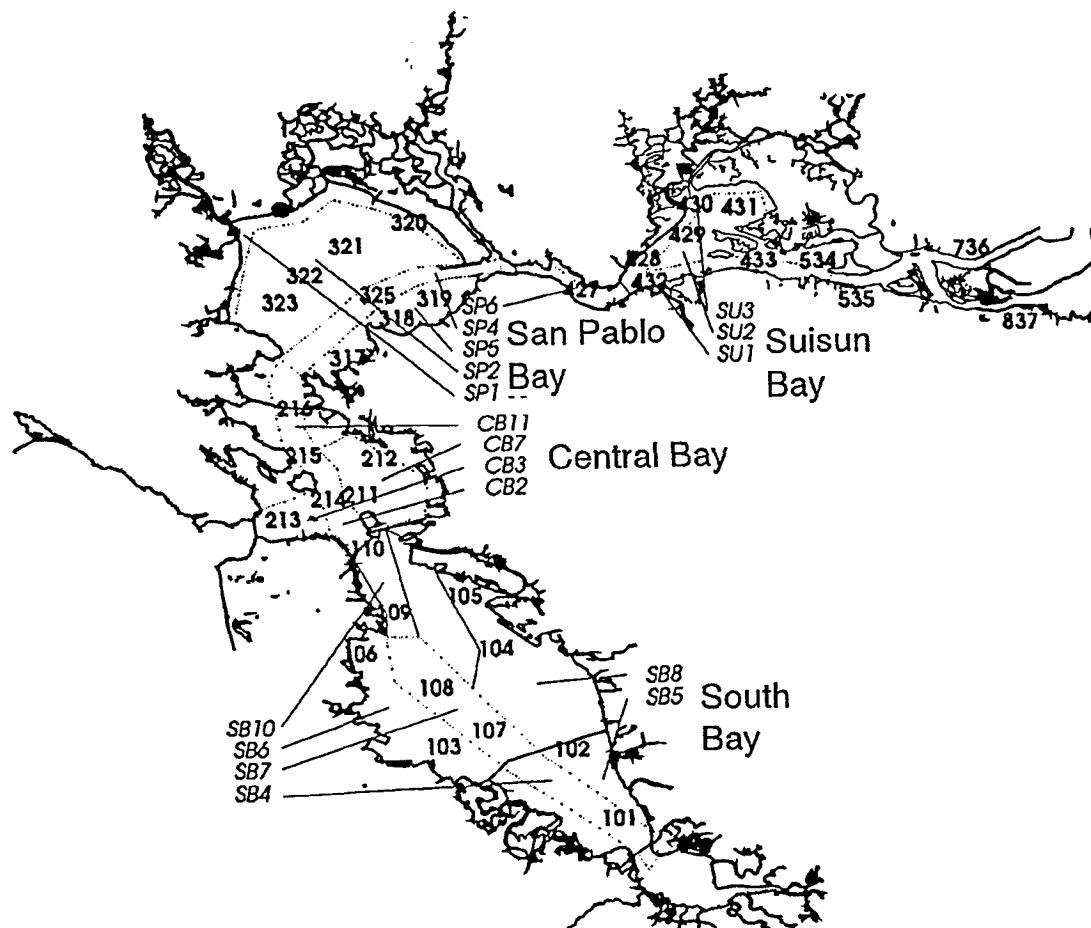


Figure 76 Sampling sites (in bold) of the CDF&G Bay Study and corresponding segments of the Bay

5.3.1 South Bay

characteristics. The ship channel passes through the sampled area of South Bay. Broad shallows south of Hunter's Point are the dominant feature of the west side. The west side receives cooling water discharges from power plants at Hunter's Point. The eastern side is dominated by the port of Oakland and by shallow areas with some beds of eelgrass. At the upper end of the region and along the east side an extensive shallow area exists (San Bruno Shoal). Coyote Creek and San Francisquito Creek are two of the streams carrying freshwater into South Bay.

Channel sites. Five stations in South Bay sample three of the channel segments, station 101 in the southernmost area below the San Mateo Bridge (segment SB4), stations 107 and 108 in the channel from San Mateo Bridge to Hunter's Point (segment SB7) and stations 109 and 110 in the channel between Hunter's Point and Central Bay (segment SB10). Depths recorded at the channel stations range from 12.6 m to 17.3 m.

Shoal sites. On the east side of South Bay, station 102 is over the mudflats between the Dumbarton and San Mateo Bridges (segment SB5), depths during sampling averaged 3.8 m. Stations 104 and 105 are in the shallows between the San Mateo Bridge and Alameda (segment SB8), depths averaged 3.3 - 3.6 m. Stations 103 and 106 are over the San Bruno Shoals (segment SB6), depths during sampling average 3.3 - 3.6 m.

General patterns: The fishes of South Bay are generally either species which are characteristic of small California lagoon estuaries where they are subjected to a narrow range of salinities or they are more truly marine species that invade seasonally (Table 9). The assemblage is dominated by northern anchovy, Pacific herring, shiner perch, jacksmelt and topsmelt, but there is little predictability in the species composition at many sites.

Two physical features appear to be associated with the consistent distribution of fishes within South Bay; depth and distance to Central Bay. Northern anchovy and Pacific herring are found in the midwater trawl at all stations, but jacksmelt and topsmelt are caught only in the midwater trawl and usually in shallow stations, as is walleye surfperch. Shiner perch, on the other hand appeared more regularly in the midwater trawls of channel sites. In the otter trawl brown smoothhounds and brown rockfish occur regularly only in channel stations. Proximity to Central Bay seems to be the main determinant of the catch of brown rockfish and leopard sharks.

Table 9. Ranks (and number of occurrence) for the six most frequently caught fish species in the 1062 pairs of midwater and otter trawls performed at ten stations in South Bay.

Species	Rank in total midwater catch	Rank in Otter trawl
northern anchovy	1 (733)	1 (559)
jacksmelt	2 (475)	
Pacific herring	3 (407)	
shiner perch	4 (262)	2 (546)
topsmelt	5 (191)	
longfin smelt	6 (123)	
bay goby		3 (353)
white croaker		4 (321)
English sole		5 (336)
speckled sanddab		6 (269)

In the midwater trawls, the channel stations show a pattern of greater consistency in catch at the stations at either end of South Bay than at stations in the middle (107 and 108). Despite large fluctuations in their abundance as they move in and out of the Bay on a seasonal basis, northern anchovy are one of the most consistent fish in the midwater catch at all South Bay stations. Pacific herring are found year round at the stations near Central Bay but are consistently present in more southerly stations only during the first six months of the year. Jacksmelt are collected regularly only in the midwater net and consistently at any one site only during the period from April to September. The midwater trawls at several stations catch longfin smelt regularly from January through March, except for the southernmost station (101) where they continue to be a regular part of the catch into the spring.

In the otter trawl catches, northern anchovies are among the most regular part of the catch at almost all stations and seasons; however, they are a much smaller part of the catch and their numbers do not show the strong seasonality of the midwater trawl catch. At all stations predictability of catch is least in the months from October to December. As with the midwater trawl, station 108 yields a much less predictable catch than the stations to the north or south. Closer to Central Bay, white croaker is commonly caught in all seasons of the year, but at the southern stations they are less dependably present in the winter. Bay goby are caught for a larger portion of the year in channel sites and generally in the spring at shallow sites.

Midwater trawls at shoal stations are very similar to those of channel stations with two exceptions: jacksmelt are caught regularly year-round (or for at least three seasons) at several shoal stations, and walleye surfperch are regularly caught at station 106 at Candlestick and station 104 near San Leandro.

Otter trawl catches at shoal stations yield fish associations that do not differ greatly from one side of the Bay to the other, but which are very different from the otter trawl catches in the channel. The fish assemblage of the shoal stations is much less predictable than that of the channel, with the period of greatest predictability limited to the months from April to June, except off Hunter's Point where the assemblage persists into the summer. The distribution of English sole also differs between the shoals and shallows. In the channel English sole are regular features of the catch for most of the year at station 110, near Central Bay, but they are not part of the regular assemblage at most of the other channel sites. At all shoal sites, however, English sole are always a regular part of the April-June assemblage.

The abundance and regularity of fishes at San Bruno Shoal could be related to the high productivity of this area of phytoplankton and zooplankton (Appendix A).

5.3.2 Central Bay

Characteristics. Most of Central Bay (segments CB11, CB3, and CB2) provides little shallow habitat so that the habitat is less heterogenous than in other embayments. Segment CB11 is one of the few areas in San Francisco Bay supporting eelgrass beds. Stations range in average depth from 10 to 24 m. Stations 211 and 212 are located in segment CB7, the shallow areas near the Berkeley mudflats, and have mean depths of 7.7 and 3.3 m, respectively.

General patterns: The dominant species of Central Bay (Table 10) are largely the same as those of South Bay, with increasing abundance of euryhaline species found in greater abundance in San Pablo Bay. The seasonal presence of chinook salmon distinguishes Central Bay from South Bay. Speckled sanddab are present in higher abundances and for more of the year than in other embayments.

Table 10: Ranks (and number of occurrence) for the six most frequently caught fish species in the 638 pairs of midwater and otter trawls performed at six stations in South Bay.

Species	Rank in midwater catch	Rank in Otter trawl
northern anchovy	1 (393)	2 (336)
Pacific herring	2 (335)	
jacksmelt	3 (211)	
longfin smelt	4 (154)	6 (311)
shiner perch	5 (134)	1 (358)
white croaker	6 (113)	4 (331)
speckled sanddab		5 (313)
English sole		3 (336)

The main feature associated with the regular species composition at sites in Central Bay proximity of San Pablo Bay or the Golden Gate; sites closer to San Pablo Bay regularly yield fish characteristic of that embayment while sites closer to the ocean yield collections with more marine species. Only one truly shallow site is sampled so it is difficult to separate the effects of depth from location. However, it appears that catch in the shoals varies seasonally more than in the channel where the same set of species predominate for most of the year. Starry flounder was a species that uniquely characterized the shallow station.

The midwater trawl is characterized in Central Bay by two species, chinook salmon and topsmelt. The seasonal catch of chinook salmon at all deepwater sites between the months of April and June, with occasional catches on an irregular basis in the months from July to September, separates all Central Bay stations from all South Bay stations. Chinook salmon smolts were absent at all stations during the rest of the year. Less obviously characterizing Central Bay is the consistent regular catch of jacksmelt without the similar topsmelt. At most stations in South Bay jacksmelt outnumber and are more frequent in their occurrence than topsmelt but stations where jacksmelt are regular are also often associated with regular catches of topsmelt. Topsmelt seem to be much less common outside of South Bay.

The deeper water habitat sampled by the otter trawl contains an abundant and diverse fish assemblage. The dominant species (English sole, shiner perch, white croaker, speckled sanddab and longfin smelt) are common for most of the year, with seasonal incursions by bay goby and plainfin midshipmen. At the more northerly stations longfin smelt rise in abundance and in frequency of occurrence.

5.3.3 San Pablo Bay

Characteristics. San Pablo Bay provides extensive shallow habitat so that the habitat is very different than Central Bay. Four stations (323, 322, 321, and 320) are arrayed in an arc across the broad shallows in the triangle formed by Point San Pedro, Tubbs Island, and Mare Island in segment SP3. South of the channel the shoals are divided into segment SP5 west of Pinole Point, where station 317 is located, and segment SP6 east of Pinole Point which contains stations 318 and 319. Only station 325 is situated in the channel where mean depths were 11 m (segment SP4), so it is not possible to identify the fish assemblage of deeper waters. All other stations are in the extensive shallows with mean depths less than 4.5 m.

General patterns. The fishes of San Pablo Bay (Table 12) consist of a set of resident estuarine species (longfin smelt, starry flounder, striped bass, and staghorn sculpin) and a set of more lagoon or marine species that invade in dry years or during the spring and summer months (white croaker, bay goby, jacksmelt, and shiner perch). The embayment is also a regular home for young English sole, Pacific herring, and white croaker.

Table 12. Ranks (and number of occurrences for the six most frequently caught fish species in the 852 pairs of midwater and otter trawls performed at eight stations in San Pablo Bay.

Species	Rank in total midwater catch	Rank in Otter trawl catch
northern anchovy	1 (539)	2 (398)
longfin smelt	2 (335)	1 (417)
jacksmelt	3 (302)	
Pacific herring	4 (300)	
striped bass	5 (207)	6 (293)
American shad	6 (155)	
starry flounder		5 (313)
shiner perch		4 (321)
yellowfin goby		3 (336)

The main feature affecting the distribution of fish within San Pablo Bay seems to be the distance to the Golden Gate. As the stations progress upstream, their fish assemblages more often contain estuarine species and less often contain oceanic species. Only one deep station is sampled (325), but its fauna appears to resemble that of the deep stations in Central Bay, noticeably in the regular seasonal presence of chinook salmon smolts, which are not regularly caught anywhere else within San Pablo Bay. Species of South Bay and Central Bay appear to invade San Pablo Bay either seasonally in the months when there is usually little freshwater outflow or occasionally in other parts of the year, when conditions are suitable. These invasive or seasonal species are principally jacksmelt, shiner perch, Pacific herring, bay goby, and white croaker. American shad are caught at most stations but only in the period from October to December. There seems to be more similarity between the stations at similar distances upstream than between stations on one side of the channel. Thus, stations 317 and 323 at the south end of San Pablo Bay are more similar to each other than to upstream stations on the same side. The same pattern is shown by stations 319 and 320 which are on the opposite sides of the channel at the north end of the bay. Of the more estuarine species, only longfin smelt are regularly found in downstream sites.

5.3.4 Suisun Bay

Characteristics. Suisun Bay provides both extensive shallow habitat and a long, deep channel that is thoroughly sampled by the Bay Study. Like South Bay, then, it is possible to examine patterns of different habitat use by species. The long channel runs close to shore on the southern side of the embayment so that almost all shallow habitat is on the north side. Channel stations (428, 429, 432, and 433) are all in segment SU1 with average depths of 8 to 10 m. Shallow stations 430 and 431 are in Grizzly Bay (segment SU2), which is adjacent to Suisun Marsh (SU4). Honker Bay (segment SU3) is a smaller, shallow embayment upstream and contains station 534.

General patterns. Carquinez Straits appear to represent a major break in the distribution of species within the estuary. Several of the regular species of Suisun Bay (Table 13) are absent from downstream sites, some are common in San Pablo Bay and more common in Suisun Bay and a number of the common species of the lower bays are absent from Suisun

Bay. Delta smelt and Sacramento splittail are regularly caught in Suisun Bay but are very rarely found downstream. The six-species assemblage (striped bass, yellowfin goby, longfin smelt, starry flounder, staghorn sculpin, and Delta smelt) found in the trawls near Grizzly Bay is a consistent and unique feature of this bay. The regular catch of white sturgeon makes Honker Bay unique. The greatly reduced abundance of northern anchovy and Pacific herring and the near absence of jacksmelt, white croaker, and bay goby are also distinctive features of Suisun Bay catches.

Midwater trawls throughout Suisun Bay are most likely to contain striped bass and longfin smelt, other species are seasonally present but in general the number of species encountered is small and the species composition of a catch is unpredictable. Otter trawl catches, on the other hand are quite predictable, and the species groups conform well to the segmentation scheme of Gunther (1987). In the deep channel (SU1) the catches are unpredictable, in Grizzly Bay (SU2) the catches are larger and the species composition is highly consistent throughout the year. In Honker Bay (SU3) the catch is very small and very few species can be expected.

Table 13. Ranks (and number of occurrence) for the six most frequently caught fish species in the 747 pairs of midwater and otter trawls performed at seven stations in Suisun Bay.

Species	Rank in total midwater catch	Rank in Otter trawl catch
striped bass	1 (729)	1 (671)
longfin smelt	2 (682)	2 (516)
northern anchovy	3 (345)	6 (149)
American shad	4 (323)	
Delta smelt	5 (262)	
yellowfin goby	6 (181)	3 (364)
starry flounder		4 (332)
staghorn sculpin		5 (321)

5.3.5 Western Delta

Characteristics. Three stations (535, 736, and 837) are on the border of the San Francisco Bay complex and the western Delta. Station 535 is below the confluence of the two rivers on Chipp's Island, station 736 is in the lower reaches of the Sacramento River, and station 837 is in the lower reaches of the San Joaquin River. Water moves among these stations, not only by river flow, but twice daily water moves up both river channels on the rising tides and, depending on outflow and diversion rates, there is a net movement of water up the lower San Joaquin from either of the other two stations.

Conditions at each site present very different environmental conditions for the fishes. At station 535 the water is often a mix of Sacramento River water and salt water. At station 736 the water is predominately Sacramento River water with limited movement of mixed water into the station on high tides. Station 837 may have any combination of San Joaquin River water, Sacramento River water flowing around Sherman Island and up the San Joaquin River, or a mixture of water moving back and forth with the tides. Depths also distinguish the three stations because 535 and 736 are over 10 m deep whereas station 837 is only 4.4 m deep on average.

General patterns. The Delta contains a mixed assemblage of euryhaline freshwater fishes (e.g. threadfin shad, white catfish, and channel catfish), euryhaline marine fishes (e.g. starry flounder and Pacific herring), estuarine fishes (e.g. Delta smelt, longfin smelt, striped bass, and yellowfin goby), and anadromous fishes (e.g. chinook salmon, American shad, and Pacific lamprey). Catches are generally low and presence of a species varies strongly with shifting physical conditions. East of these two stations there is a separation in the general distribution of native and introduced species (Sazaki 1975; DFG 1987a; Herbold and Moyle 1989). The warmer and more saline waters of the San Joaquin River are usually inhabited by introduced species while the north Delta, dominated by waters of the Sacramento River, is the only place where most native species can be found.

Table 14. Ranks (and frequency of occurrence) for the six most abundant species fish species in the 214 pairs of midwater and otter trawls of the CDF&G Bay Study at stations east of Suisun Bay.

Species	San Joaquin midwater	otter	Sacramento midwater	otter
red bass	2 (41)	1 (87)	1 (65)	1 (49)
can shad	1 (49)		3 (26)	2 (28)
in smelt			2 (51)	
smelt	4 (23)		4 (34)	
fin goby		3 (10)	5 (16)	5 (19)
ok salmon	5 (23)		6 (17)	
dfin shad	3 (26)			
c herring	6 (3)			
flounder		2 (36)		
catfish				3 (30)
el catfish		4 (12)		6 (22)
sturgeon				4 (13)
ale logperch		5 (15)		
il		6 (14)		

5.3.6 General patterns: comparisons across areas

Some species are characteristic of each section of the Estuary (Figure 75). Carquinez Straits, with its high velocities and diverse conditions of salinity and temperature, appears to be a barrier for many fish species. Several abundant species occur in abundance only on one side or the other.

South Bay is the only embayment where topsmelt and brown smoothhounds are regularly found at particular stations. Chinook salmon and American shad do not occur regularly anywhere in South Bay but are seasonal components of all upstream embayments. Bay gobies are found for most of the year at some sites in South Bay but are more seasonal in their occurrence in Central and San Pablo bays and are never found regularly at any site in Suisun Bay.

Central Bay is characterized by a rich assortment of species in the otter trawl, entering from the lagoon-like South Bay, from the more freshwater regions of San Pablo Bay and from the ocean. Speckled sanddab is more abundant, and occurs more regularly in Central Bay than in other embayments. English sole and starry flounder appear to prefer stations of different depth, with starry flounder found regularly only in shallow sites in Central Bay. Anadromous species must, of course, pass through Central Bay; but only chinook salmon smolts are regularly caught at the sampling sites.

San Pablo Bay catches reflect a characteristic assemblage of euryhaline species that is seasonally invaded by lagoon species from South Bay and marine species. The year-round assemblage consists principally of longfin smelt, starry flounder, striped bass, and staghorn sculpin. Regular invaders in the spring and summer months from downstream include

jacksmelt, white croaker, bay goby, and shiner perch. San Pablo Bay is also used as nursery grounds for English sole and Pacific herring (as well as Dungeness crab). Anadromous species must pass through, including American shad and chinook salmon. American shad are found in the shallow of the north side of the embayment whereas salmon are usually taken at the channel site. The absence of American shad from Central Bay is probably a reflection of the absence of any sampling site in the shallows around Richardson Bay or Paradise Cove.

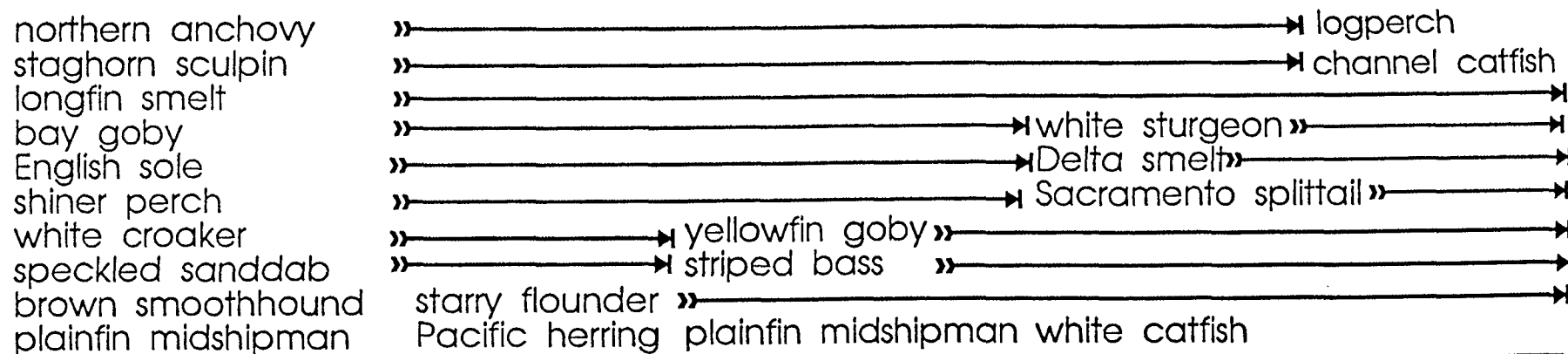
Suisun Bay supports the most distinctive fish assemblage. Striped bass, longfin smelt, Delta smelt, starry flounder, yellowfin goby, and staghorn sculpin are a consistent set of species in the shallows of Suisun and Grizzly bays. Unlike South Bay, the channel stations are much less predictable than the shallow stations. White sturgeon, Delta smelt, and splittail are not caught consistently downstream. Jacksmelt, English sole, and bay goby are three species that are abundant downstream but occur very rarely in Suisun Bay.

The western Delta stations support very few species and very few individuals compared to most downstream stations. The San Joaquin River station, probably due to stresses caused by the diversity of kinds of water that regularly flow through it, supports very few species. In the midwater trawl only migratory species consistently occur in the catch, except for threadfin shad, which are probably washed out from above. The regular catch of bigscale logperch in the otter trawl makes this station distinctive. The Sacramento River station also yields only migratory species in the midwater trawl, but they generally occur in larger numbers and more consistently than the San Joaquin River station. White catfish are regularly caught only at this site.

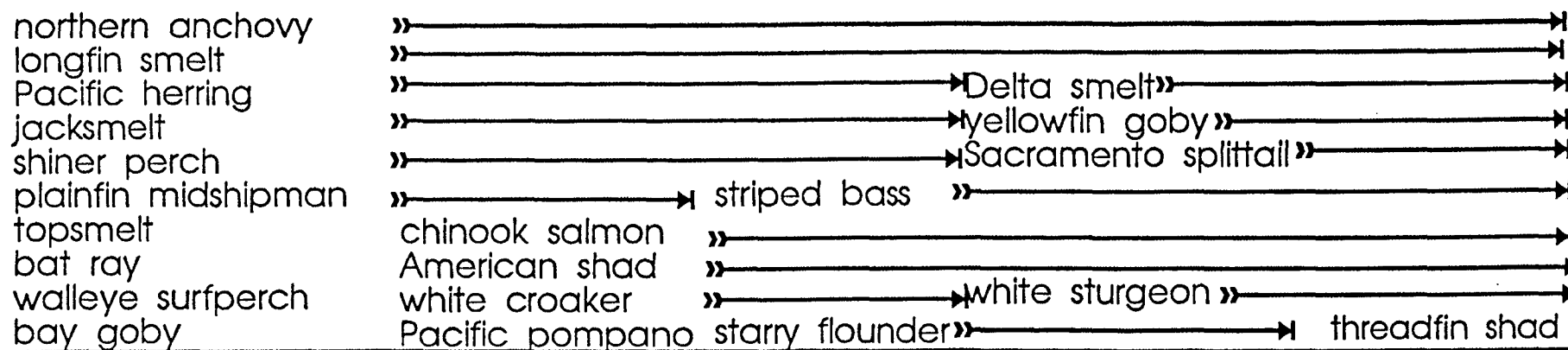
Overall, the pattern of species diversity and consistency shows a lower Bay that is regularly occupied by many species that move around seasonally along the channels. Some move into shallow stations while others remain in the channel. Fish that move into or through the Bay to spawn or whose young enter the bay from ocean spawners include plainfin midshipmen, English sole, Pacific herring, American shad, and chinook salmon. Occasional invaders of the bay that optionally spawn in the bay include white croaker, brook rockfish, and brown smoothhound. Fishes of the coastal region and lagoons that concentrate in the South Bay but move into other embayments when salinities stabilize in spring and summer include jacksmelt and bay goby and, to a much smaller extent, topsmelt. The fluctuating salinities of the upper bay and western Delta, and the narrowness of Carquinez Straits greatly reduce the diversity of species; but the species that can deal with fluctuating salinities comprise a consistent assemblage that shows little seasonality aside from movements to spawn.

Ignoring differences due to season and depth still permits identification of characteristic groups of species in each embayment (Figure 77).

Most Frequent Species in Otter Trawls



Most Frequent Species in Midwater Trawls



South

Central

San Pablo

Suisun

West Delta

Figure 77 Ten most frequently captured species in each embayment 1980-1988;
data from CDF&G Bay Study.

6.4 Analysis of status and trends within groups of fishes

The distribution of fishes within the Estuary described in Appendix B is based on the occurrence of a species in at least one-third of the trawls made at a site. In many cases these species changed in frequency of catch from very common in one-half of the decade and much less common in the other half. This section describes these trends in abundance across years.

Most research on Bay fishes has focussed on identifying how species respond to outflow. Many of the studies on striped bass have explored the hydraulic mechanisms by which moderate outflows lead to the best larval survival in striped bass (Turner and Chadwick 1972; Chadwick et al. 1977; Stevens 1977; Stevens 1979; Herrgesell et al. 1983; Stevens et al. 1985). Stevens and Miller (1983) identified chinook salmon, American shad, and longfin smelt as 'wet year' species that increase in abundance in wet years. Daniels and Moyle (1983) showed that Sacramento splittail reproduce more successfully in wetter years and tied this, at least partly, to that species' need for flooded vegetation on which to lay their eggs. The Bay Study (Armor and Herrgesell 1985; CDF&G 1987) identified how several species of fishes in the Bay responded to periods of high outflow; positive species were more abundant in wetter years, negative species were more abundant in drier years and species which showed no consistent trends were described as having a mixed response. These classifications were only based on the first five years of the study and do not include any of the responses shown during the prolonged recent drought (Table 15). Pearson (1989), studying fish of the South Bay over some of the same years and earlier, identified a somewhat different collection of species characteristic of wet and dry years (Table 15). Pearson suggested that the discrepancies were due to the limited geographic nature of his study and the less intensive nature of the Bay Study.

Table 15. Species abundance responses to increased Delta outflows into south San Francisco Bay compared to analysis by the California Department of Fish and Game (after Pearson 1989)

Species	Pearson	CDF&G
Northern anchovy	Slightly negative	Mixed response
English sole	Positive	Mixed response
Shiner surfperch	Positive	Mixed response
Goby family	Slightly negative	Positive
Staghorn sculpin	Positive	Slightly positive
Pacific herring	Positive	Slightly positive
White croaker	Negative	Mixed response
Starry flounder	Slightly positive	Positive

We examined the grouping of species in the Bay Study and Fall Midwater Trawl data sets graphically and with principal components analysis. The graphs clearly indicate general changes in the catch in each embayment for each year. The principal components indicate which species covary across years, independent of their relative abundances. Because of the log-normal distribution of species within most communities, the graphs of abundance generally show only the changes in the most abundant species. Such graphs are useful here because species composition has changed drastically through time for some embayments while remaining relatively constant in others.

6.4.1 Graphic Analysis

Graphing the abundant species in the midwater trawl for each embayment, and excluding anchovy, produces a clear picture of trends across the nine years. These figures present the total catch for each species in each year. Interannual variability is extremely high for most species. Anchovy are excluded from these graphs because their abundance seems to be tied more to oceanic conditions and they seem to be very mobile within the Bay so that their abundance in one area does not accurately reflect their patterns of abundance in the Bay overall.

South Bay. In South Bay there has been a general increase in abundance of several species, particularly white croaker and plainfin midshipmen (Figures 78 and 79). The correlation of white croaker with the passing of time is the only significant association of any abundant species of South Bay ($r=.90$; $p<.01$). Jacksmelt and topsmelt are found in most Pacific coast estuaries (Moyle 1976; Wang 1986) and have long been recognized as characteristic fishes of South Bay (Ganssle 1966; Baxter 1966; Aplin 1967). Jacksmelt and shiner perch have been the least variable species. Topsmelt have particularly blossomed in abundance in two of the dry years, but show little consistency in abundance from year to year. In the early years of the decade Pacific herring were more variable in their abundance and the drought conditions seem to have promoted a stabilization in numbers at a level intermediate to that shown earlier. Although it rises and falls, the total catch in South Bay has increased but without much change in species composition. An exception is the brief domination of the catch by longfin smelt in 1983, apparently due to simple washout from upstream in that exceptionally wet year.

The otter trawl catch in South Bay shows weak patterns among the abundant species. White croaker show elevated abundances in the last three years, but earlier years show wide variability. Bay goby show a similar pattern of consistently high abundance from 1986 to 1988, but earlier years attained similar abundances in some years. As in the midwater trawl, the onset of the drought coincides with a more consistent catch of shiner perch, but in the otter trawl the catch in 1988 was at a lower level than in most preceding years. English sole show a contrary pattern of much greater variability in later years. Bay goby and speckled sanddab show almost identical patterns of apparent multi-year cycles of abundance. Staghorn sculpins appear to vary widely but with more consistency from year to year than other widely varying species, steadily increasing to ten times their abundance from 1981 to 1985 and then steadily declining.

Overall, there is little overall change in the composition or abundance of the South Bay fish fauna except increasing abundance of white croaker.

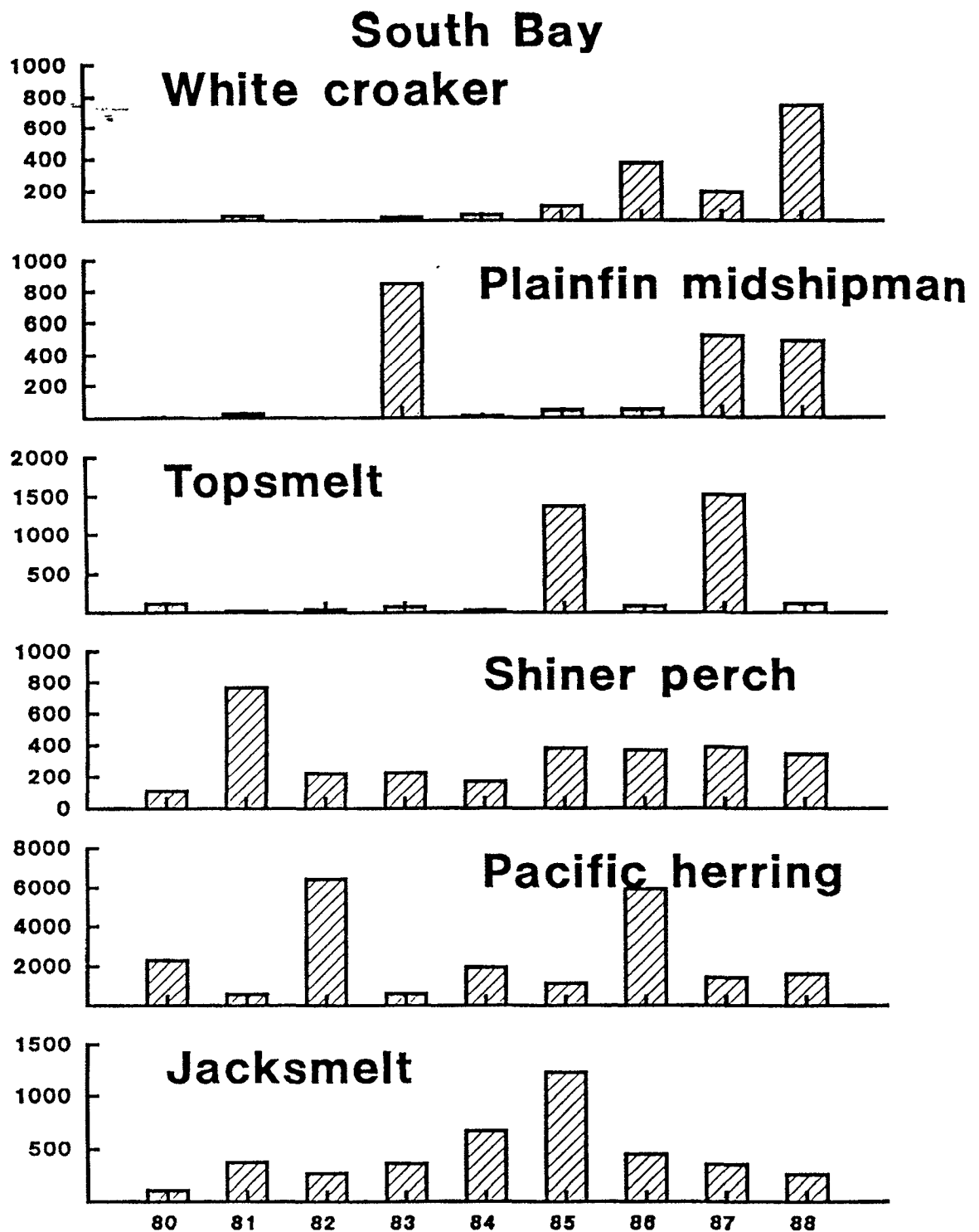


Figure 78 Catches of six dominant species of South Bay in midwater trawls across years (Northern anchovy excluded).

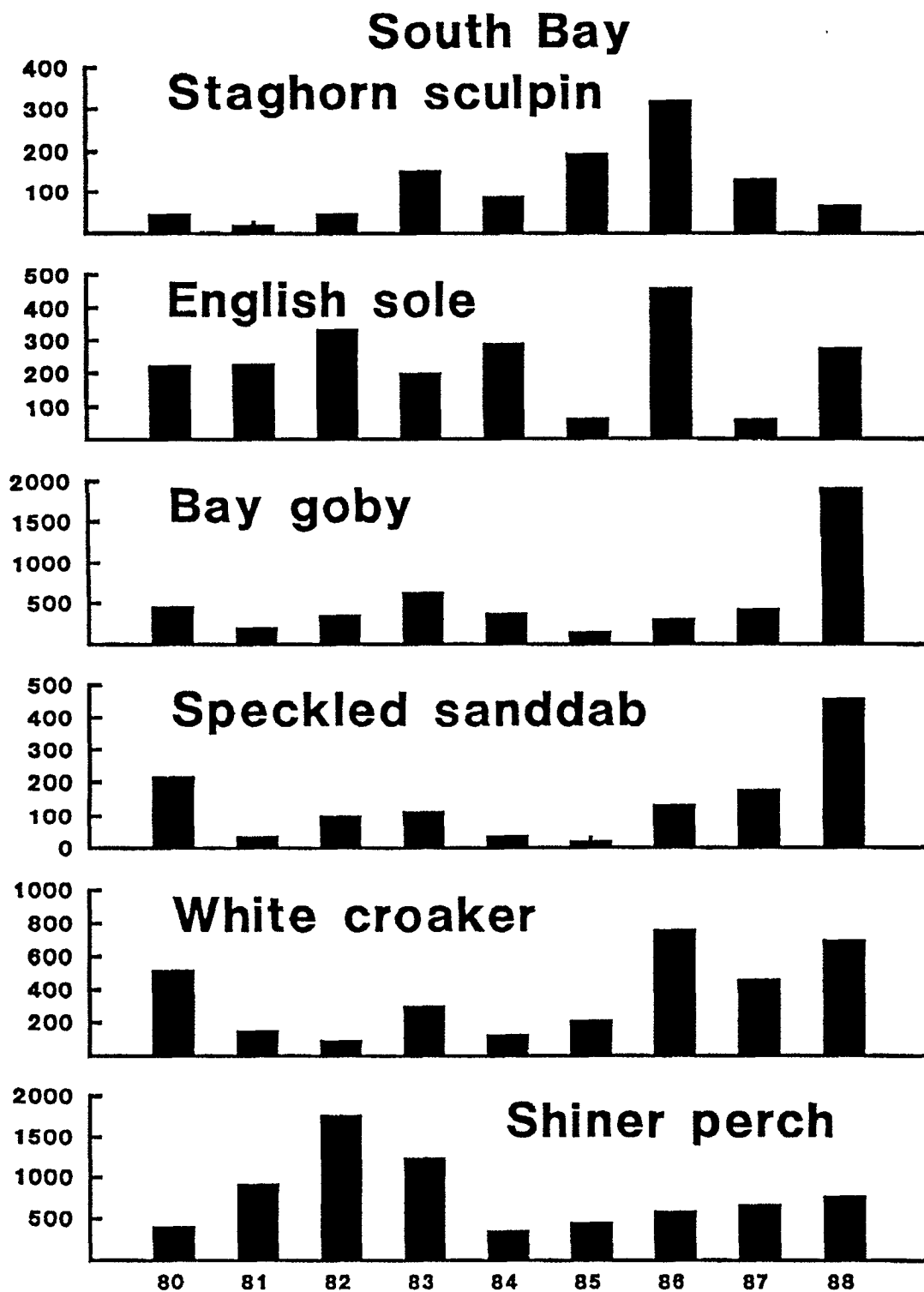


Figure 79. Catches of six most frequently captured species of South Bay in otter trawls of the Bay study through time. Northern anchovy excluded.

Central Bay. In Central Bay the midwater catch is quite variable, with no species showing any pattern of abundance through time (Figure 80). As in South Bay, white croaker shows strong increase in abundance ($r=.90$; $p<.01$). Shiner perch again are the least varying element of the catch, as they were in South Bay midwater trawls. Longfin smelt showed peaks in abundance in 1980 and 1983, which are much higher than any catch since 1984, but abundances were also very low in 1981 and 1982. Pacific herring and jacksmelt vary widely, and seemingly unpredictably, from year to year.

The otter trawl catch in Central Bay reflects several clear trends among the abundant species (Figure 81), a surprising result considering the presumed movements of many species through Central Bay. The changes in abundance from year to year are smaller than found in any other embayment. The steady rise and decline of staghorn sculpins that was seen in South Bay is exceptionally smooth in Central Bay. The increasing catch of white croaker in South Bay occurs in Central Bay as well ($r=.83$; $p<.01$) and seems to be a steady change unaffected by high outflows of 1983 and 1986. Longfin smelt show an almost equally smooth decline in catch across years, without the sharp peaks shown in the midwater trawl ($r=-.68$; $p < .05$). The rise and fall of bay goby, English sole, and shiner perch populations do not appear to be in synchrony with major environmental variables or with each other.

Overall, there are few trends across time except for the decreasing abundances of longfin smelt and the increasing abundance of white croaker.

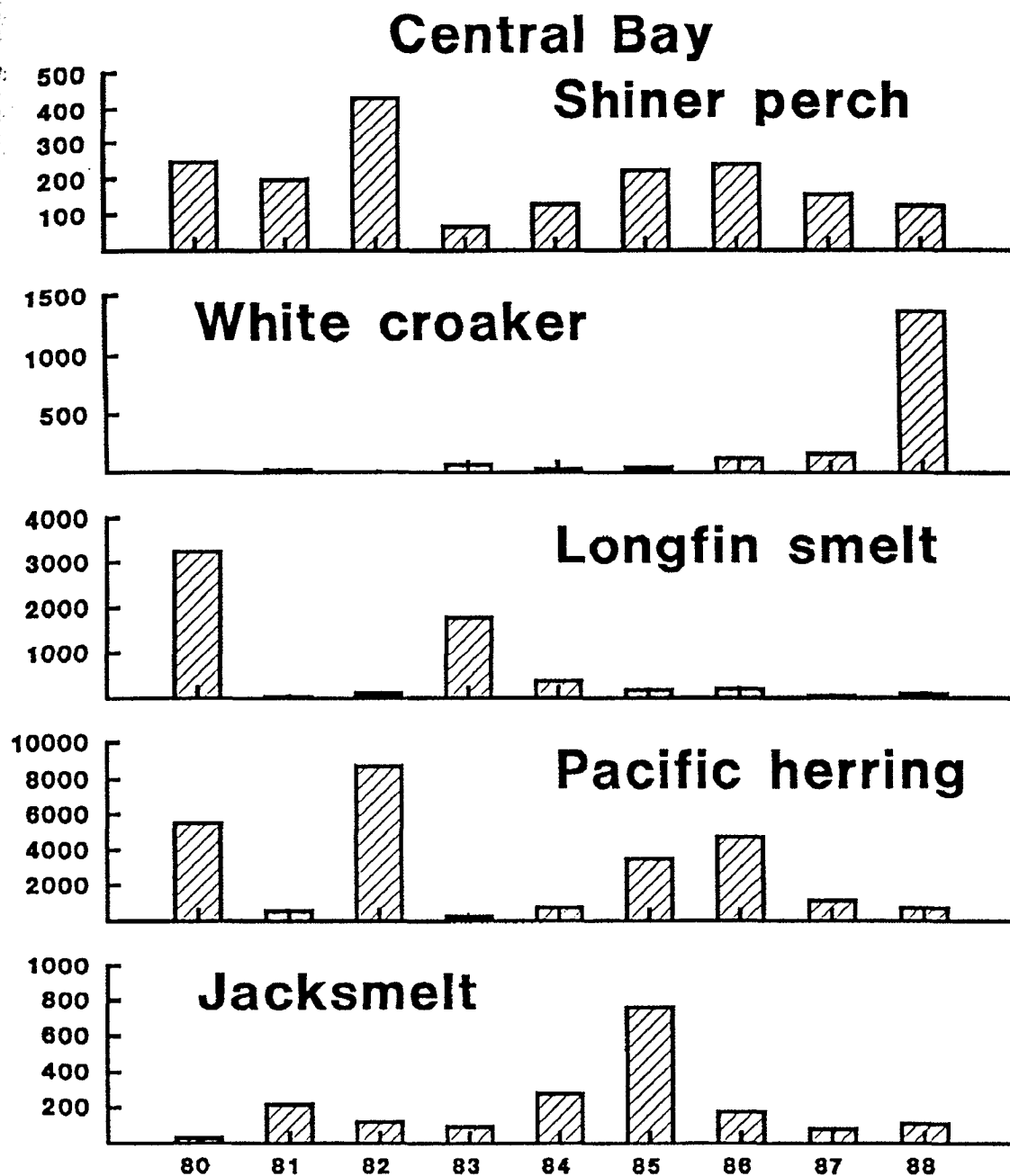


Figure 80. Catches of five most abundant species of Central Bay in midwater trawls of the Bay study through time (Northern anchovy excluded).

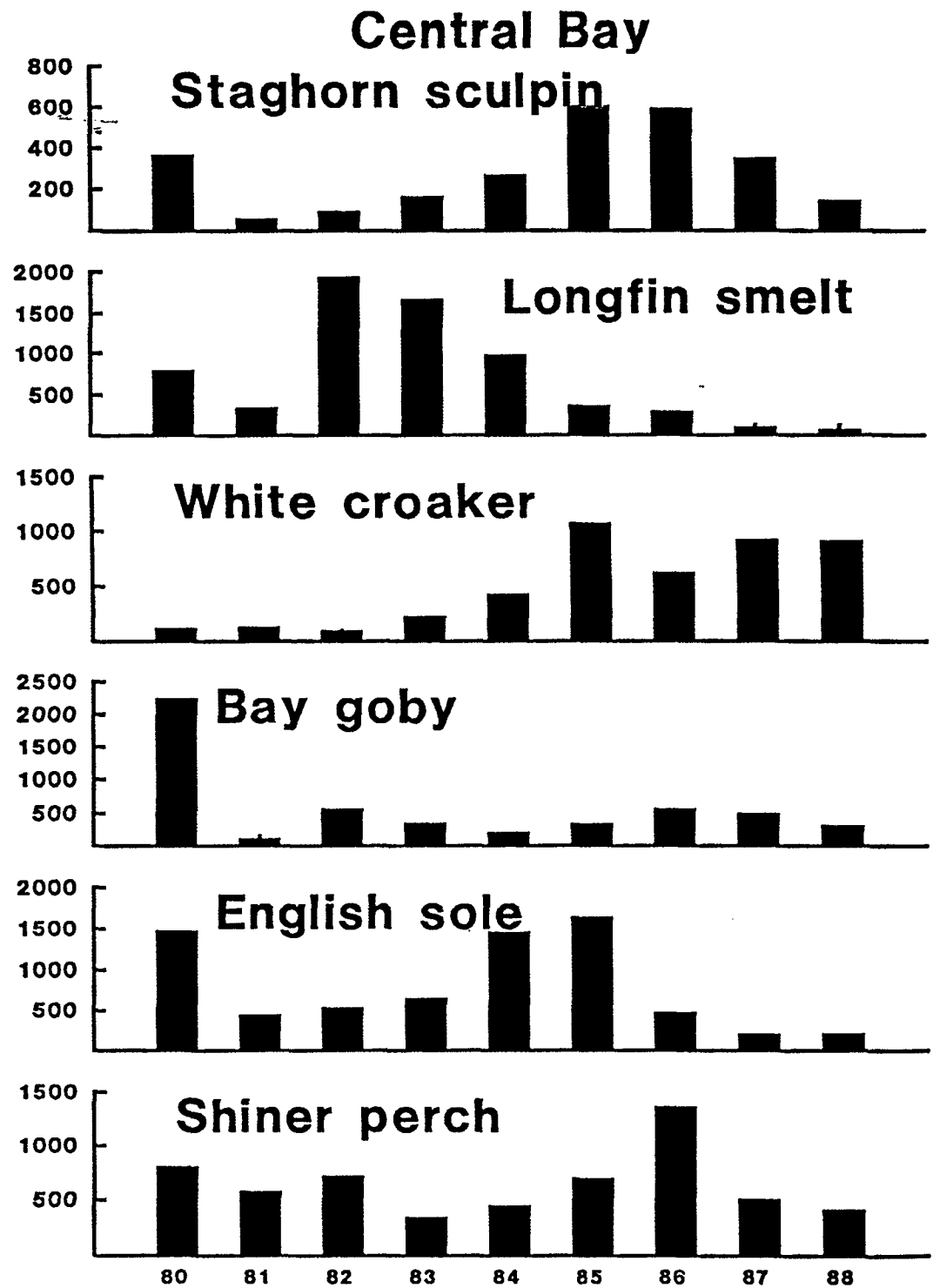


Figure 81 Catches of the six most frequently captured fishes in Central Bay in the otter trawls of the Bay Study (northern anchovy excluded).

San Pablo Bay. The midwater trawl catch from San Pablo Bay is highly variable and shows no patterns common among species (Figure 82). The decline of longfin smelt is the only obvious trend ($r=.67$; $p<.05$). In the otter trawl (Figure 83), the characteristic species of San Pablo Bay, longfin smelt and starry flounder, share a significant pattern of decline (for longfin smelt $r=-.85$, $p<.01$; for starry flounder $r = -.78$, $p<.05$). Both species show similar responses to wet and dry years in the first half of the decade. Longfin smelt, starry flounder, striped bass, and staghorn sculpin all show positive responses to years of higher outflow (Spearman's $r = .80$, $.82$, $.83$, and $.68$, respectively). Anomalously low catches characterize most species in 1985.

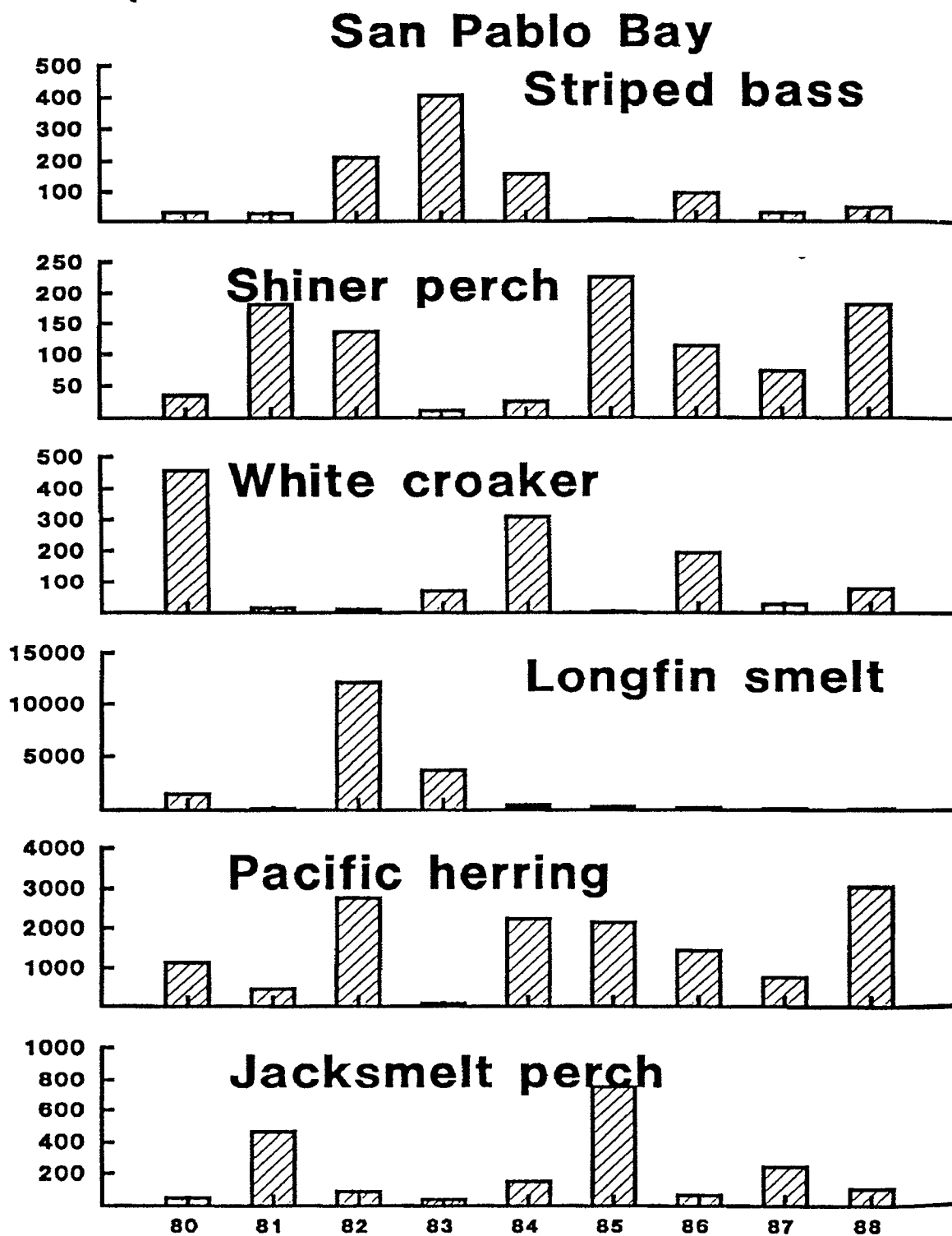


Figure 82. Catches of six most abundant species of San Pablo Bay in midwater trawls of the Bay study through time (northern anchovy excluded).

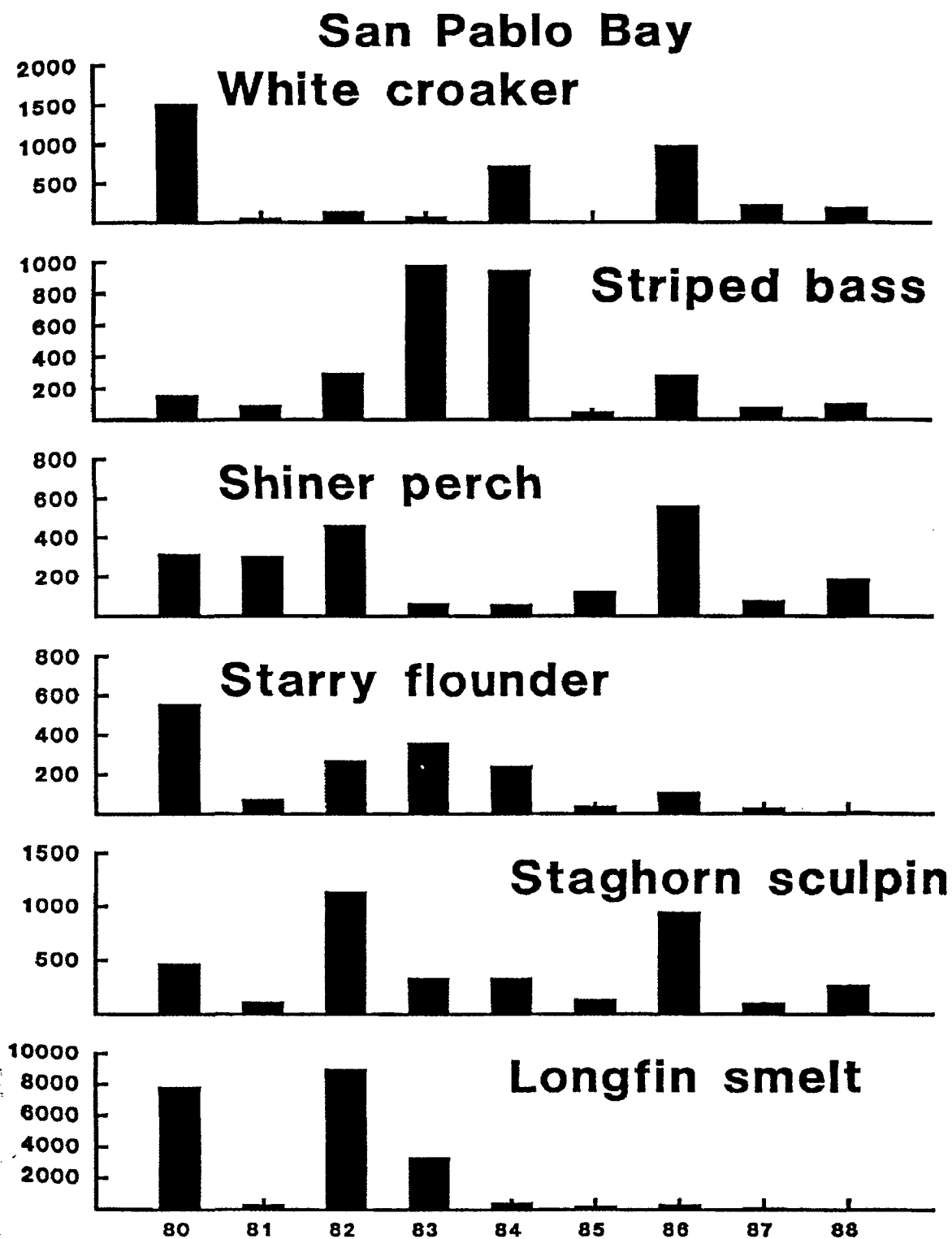


Figure 83. Catches of six most abundant species of San Pablo Bay in otter trawls of the Bay study through time (northern anchovy excluded).

Suisun Bay. Two patterns are shown in the midwater catch for Suisun Bay (Figure 84). Striped bass and American shad show their greatest abundance in 1982 and decline to record lows in the last four years of the study; the correlation with year, however, is not significant. Delta smelt and longfin smelt differ from American shad and striped bass in that they had high abundances throughout 1980-1983 and show a sharp decrease in abundance in later years. The correlation of abundance for these two species with passing years is significant (longfin smelt $r = -.80$, $p < .05$; Delta smelt $r = -.85$, $p < .01$). Pacific herring are extremely variable in abundance in Suisun Bay with no association with outflow or year, although the very high outflow of 1983 apparently prevented herring from entering Suisun Bay. The midwater trawl catch in Suisun Bay is similar to that of San Pablo Bay (Figure 85). Starry flounder and longfin smelt show significant declines through time (starry flounder $r = -.87$, $p < .01$; longfin smelt $r = -.88$, $p < .01$). The abundance of striped bass is similar to that in the midwater trawl, differing in the absence of the small peak shown in the midwater trawl in 1986. White sturgeon show a similar pattern from 1982 onward, but with very small catches in the first two years of the study. Staghorn sculpin fluctuate over a wide range in the first four years of the study but seem to have stabilized at high levels in the last five years. Yellowfin goby vary widely from year to year.

Suisun Bay

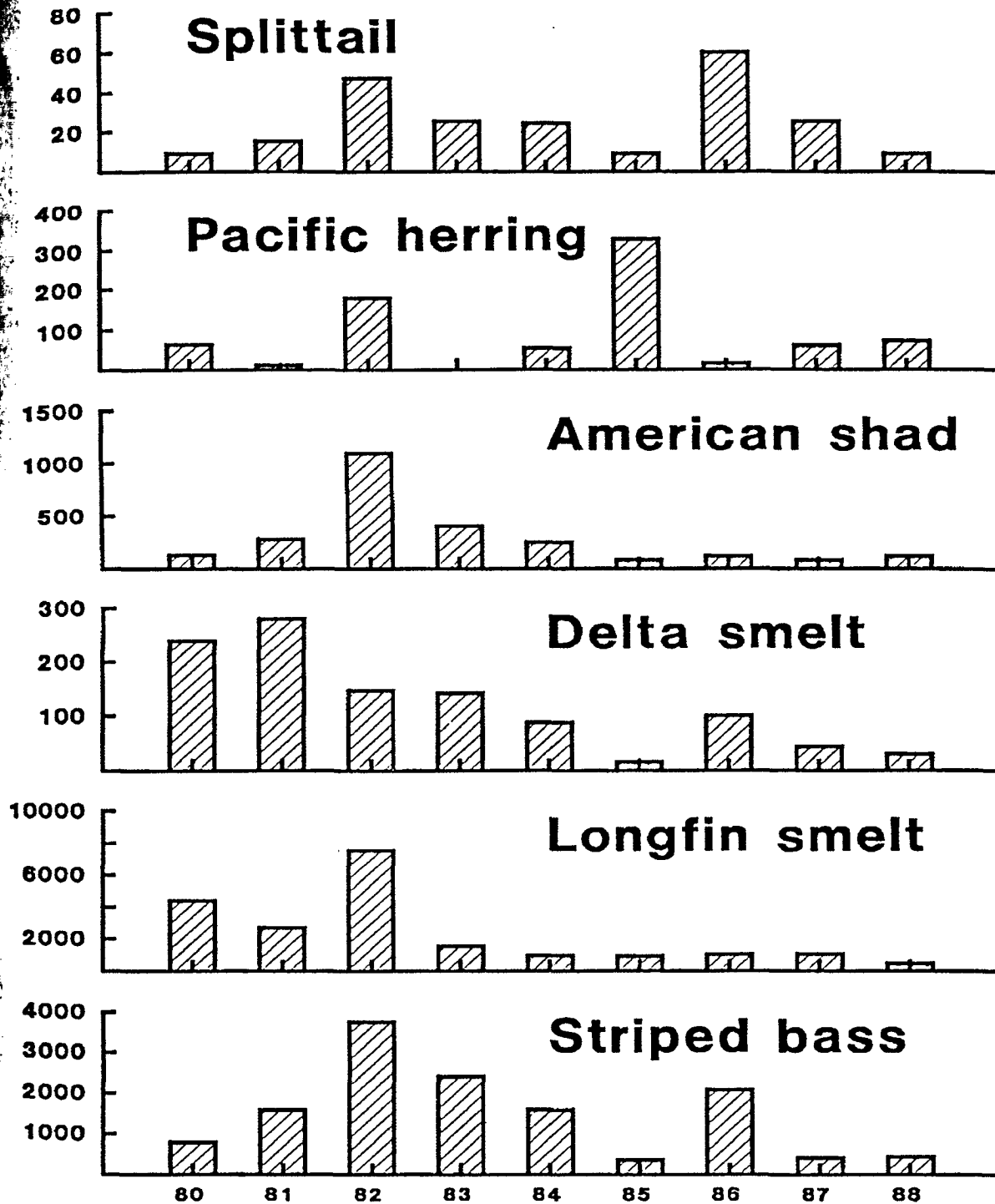


Figure 84. Catches of six most abundant species of Suisun Bay in midwater trawls of the Bay study through time (northern anchovy excluded).

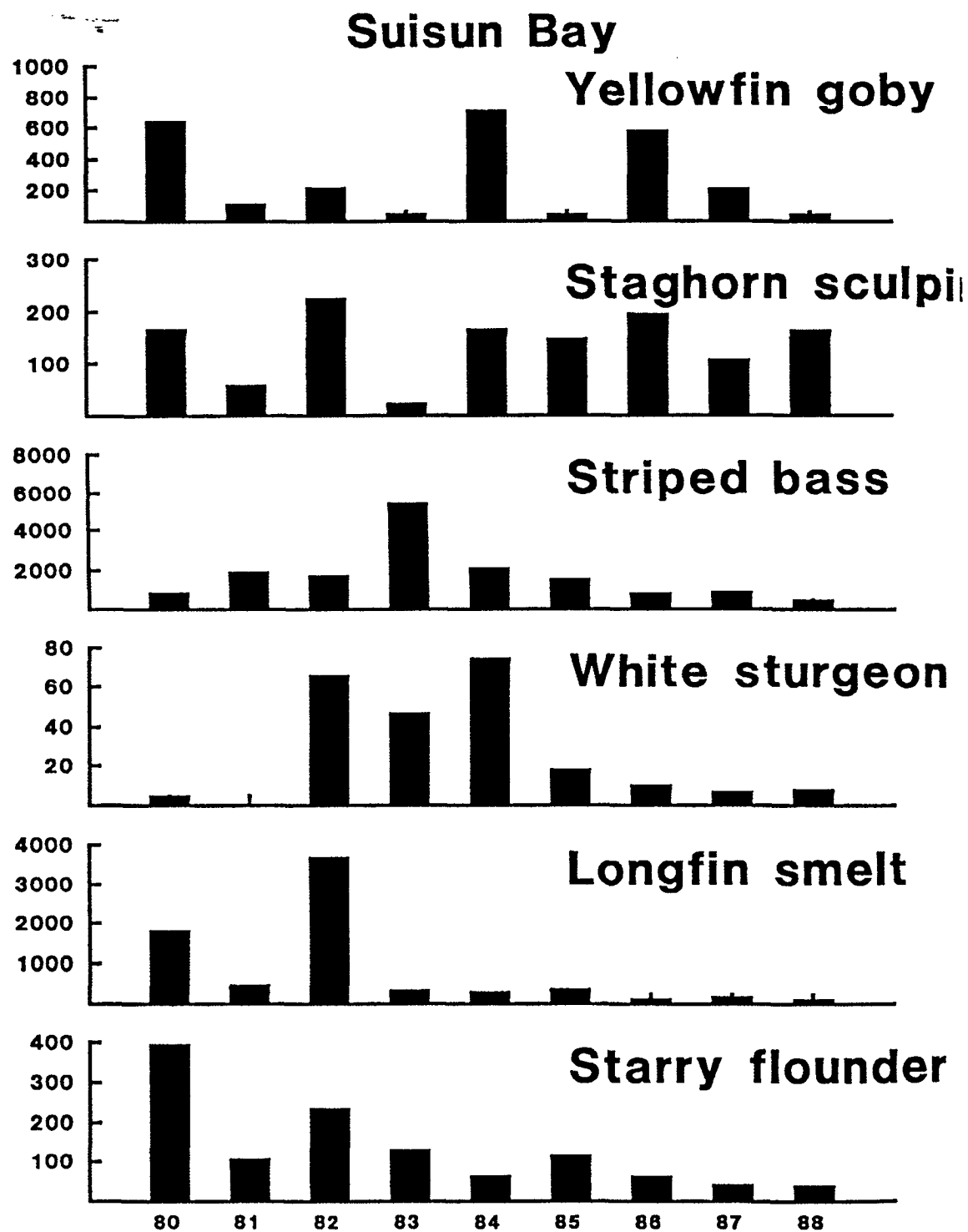


Figure 85. Catches of six most regularly caught species of Suisun Bay in otter trawls of the Bay study through time (northern anchovy excluded).

5.4.2 Update of patterns in data from the bay study

Since 1988 the bay study has not sampled in all months as it had previously. Only the months from February through August have been sampled in all years. These omissions therefore reduce the information on fall and winter time species and prevents easy comparison with the fall midwater trawl. Figures 86 to 93 present the total catch of the most abundant species in each embayment for all stations that were sampled in all years (exclusive of northern anchovy).

The two principal patterns seen in earlier years, declining abundances of most species of San Pablo and Suisun bays and the upstream spread of species characteristic of South Bay, have continued through 1989 and 1990. Longfin smelt, delta smelt, starry flounder, and striped bass are the species showing continued dramatic declines through the period. White croaker, bay goby, and plainfin midshipman have continued to show elevated abundances and increased distribution.

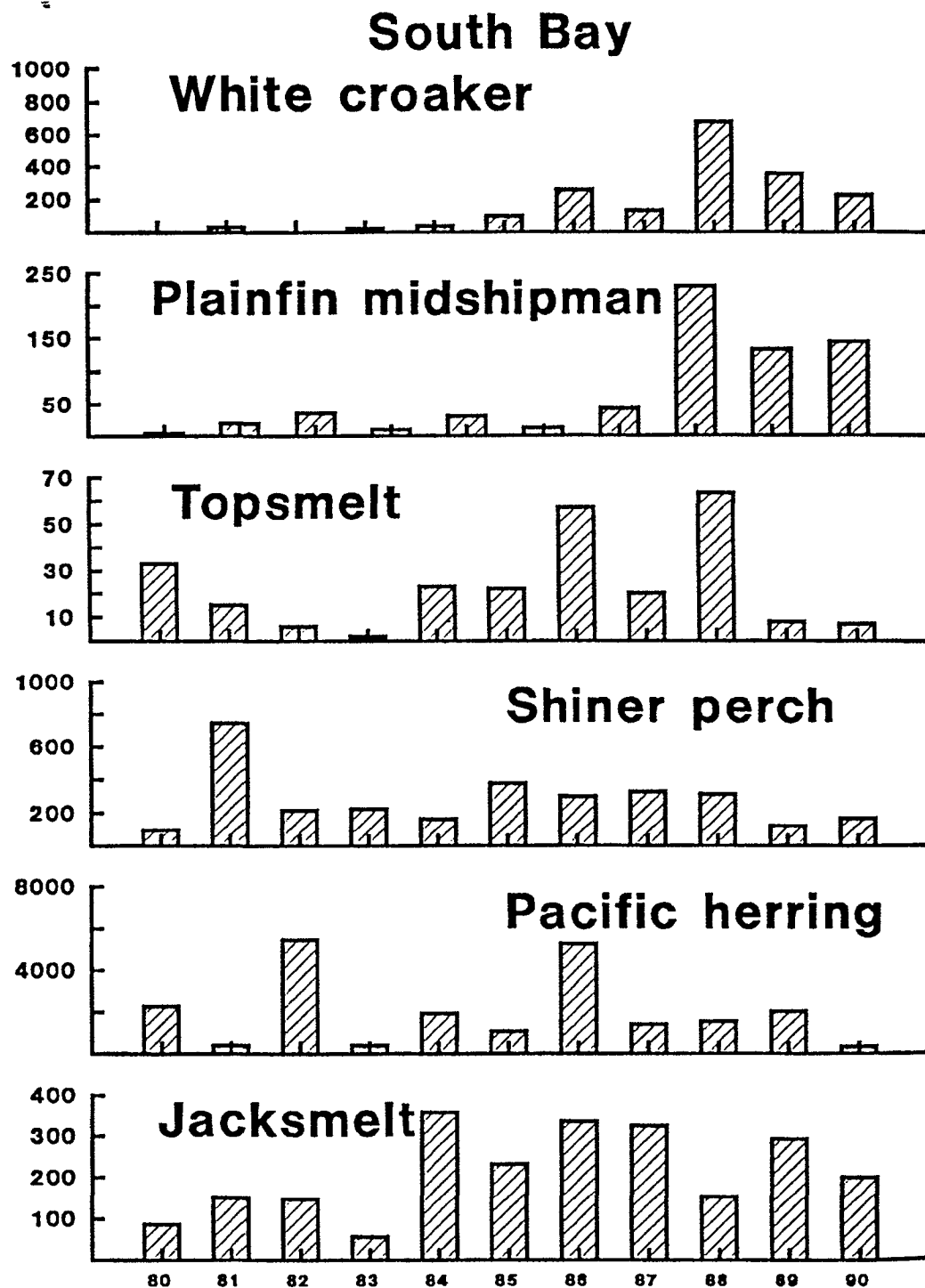


Figure 86. Midwater trawl catches of the bay study for the months of February through August in South Bay.

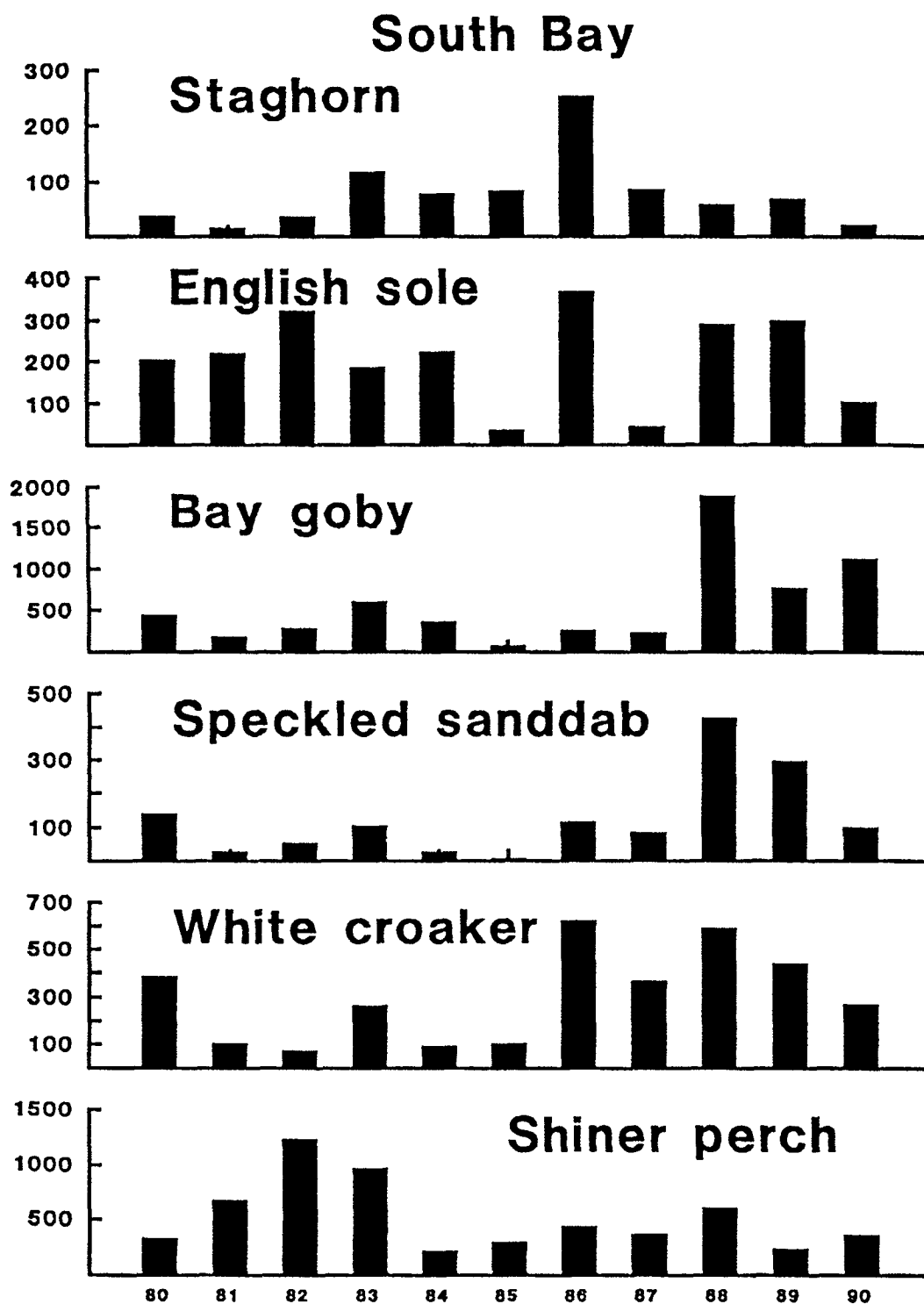


Figure 87. Otter trawl catches of the bay study for the months of February to August in South Bay.

Central Bay

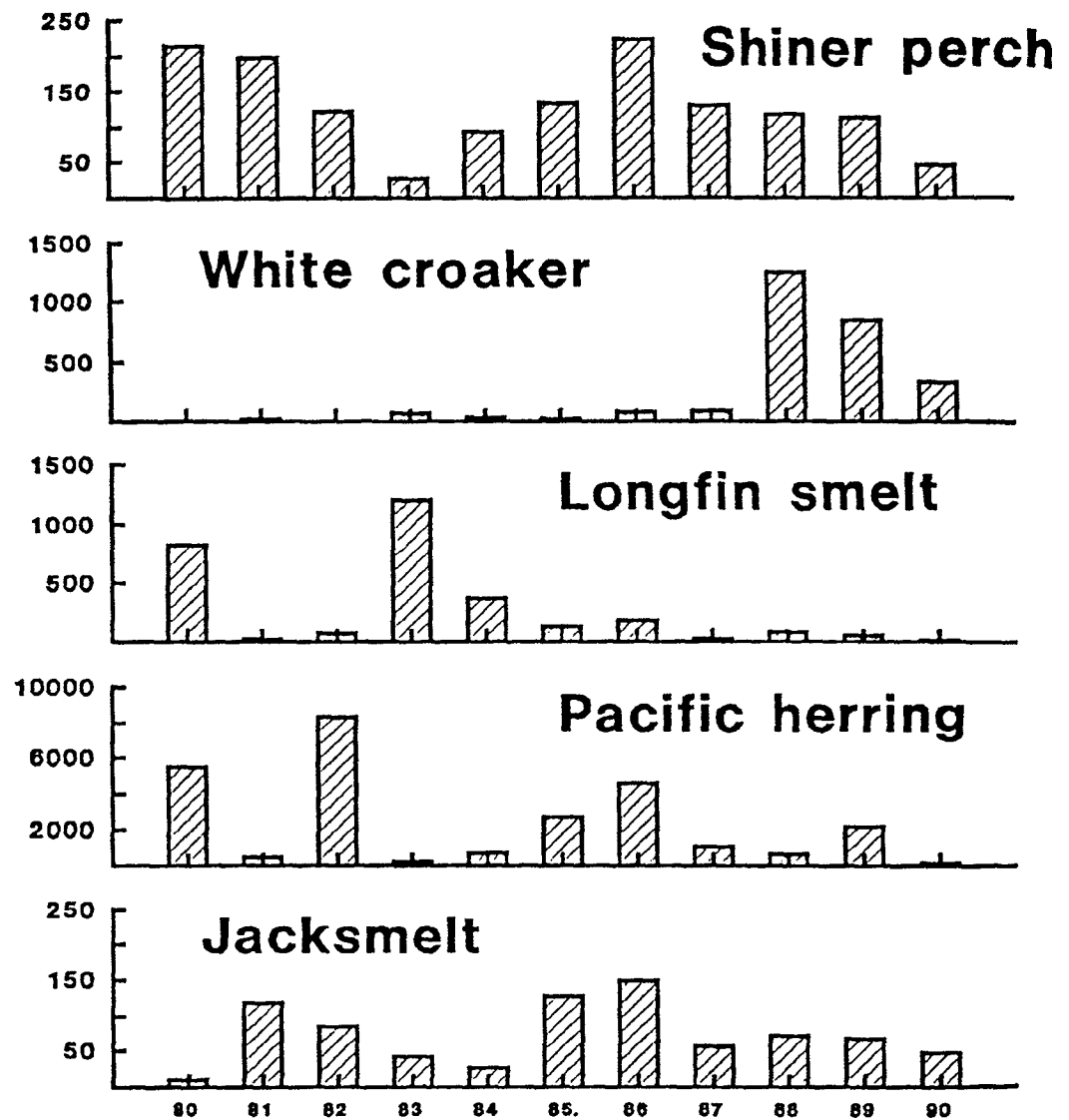


Figure 88. Midwater trawl catches of the bay study for the months of February August in Central Bay.

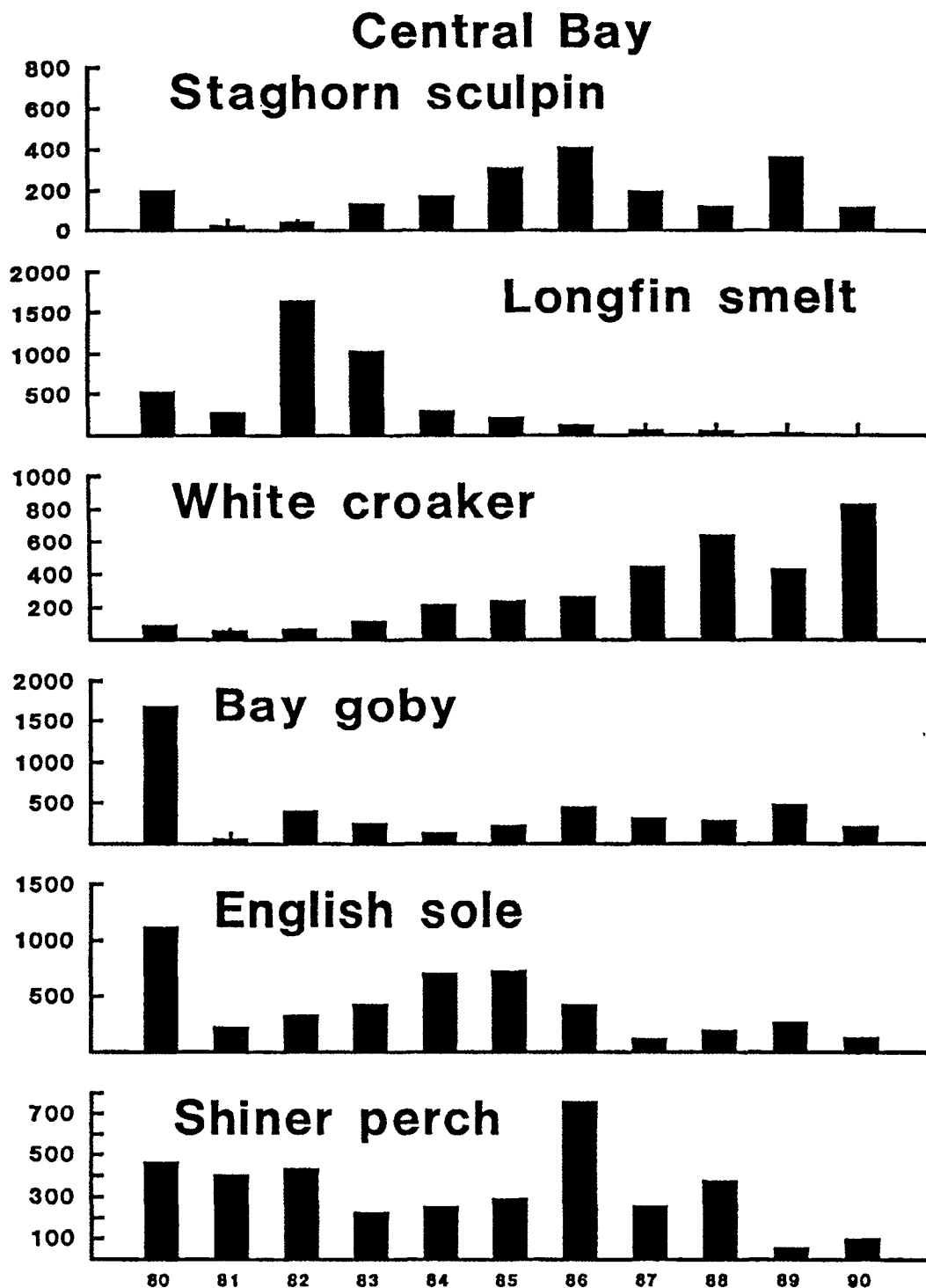


Figure 89 Otter trawl catches of the bay study for the months of February to August in Central Bay.

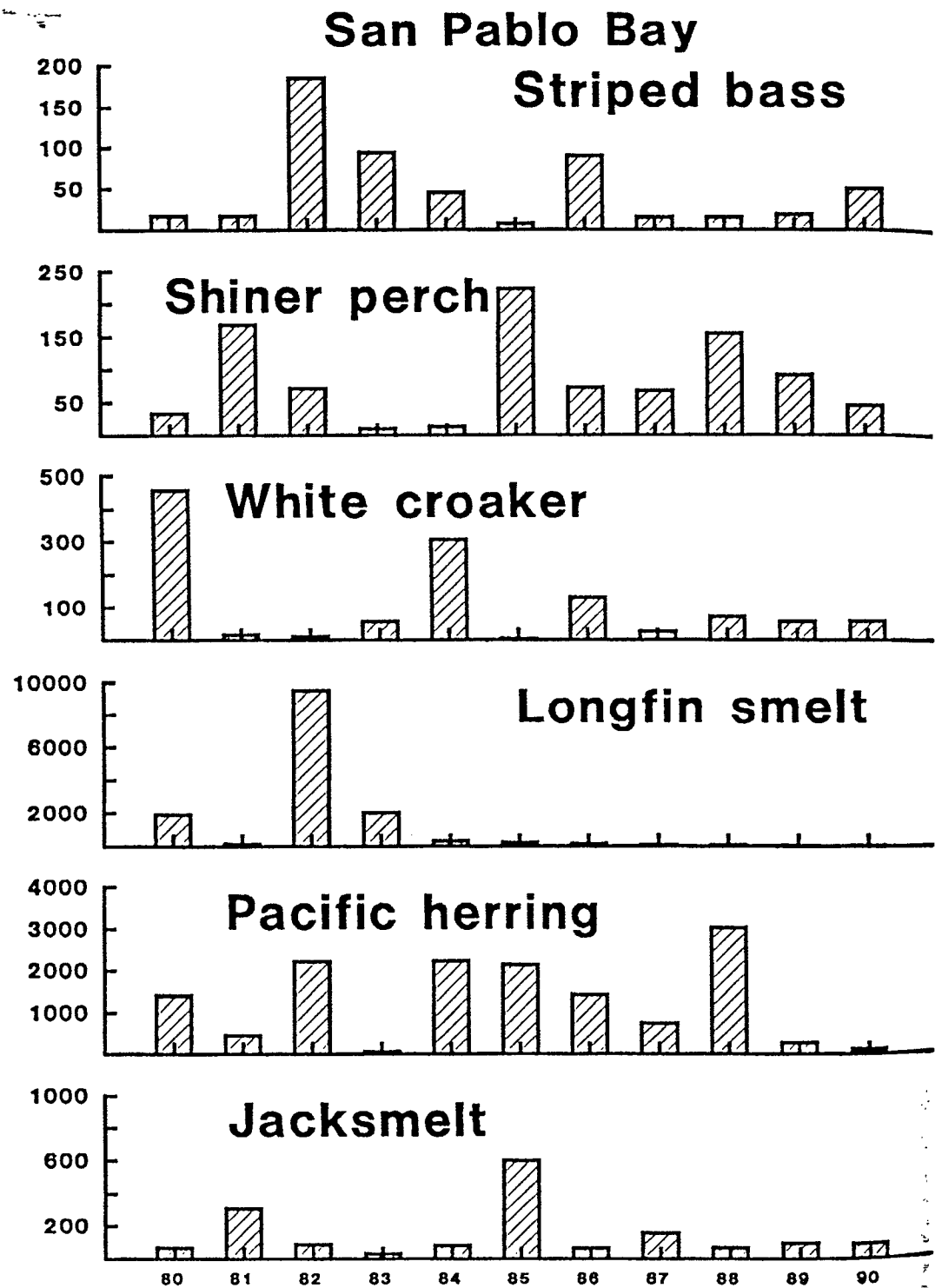
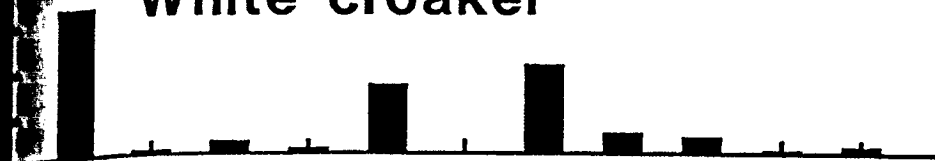


Figure 90 Midwater trawl catches of the bay study for the months of February-August in San Pablo Bay.

San Pablo Bay White croaker



Striped bass



Shiner perch



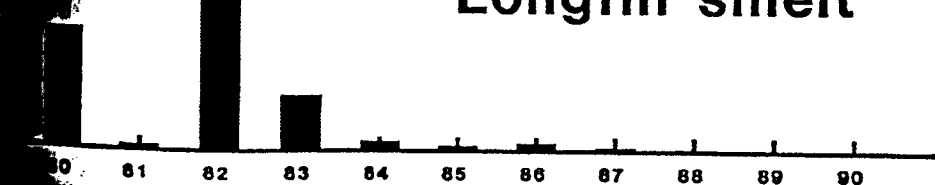
Starry flounder



Staghorn



Longfin smelt



Off-trawl catches of the bay study for the months of February to
San Pablo Bay.

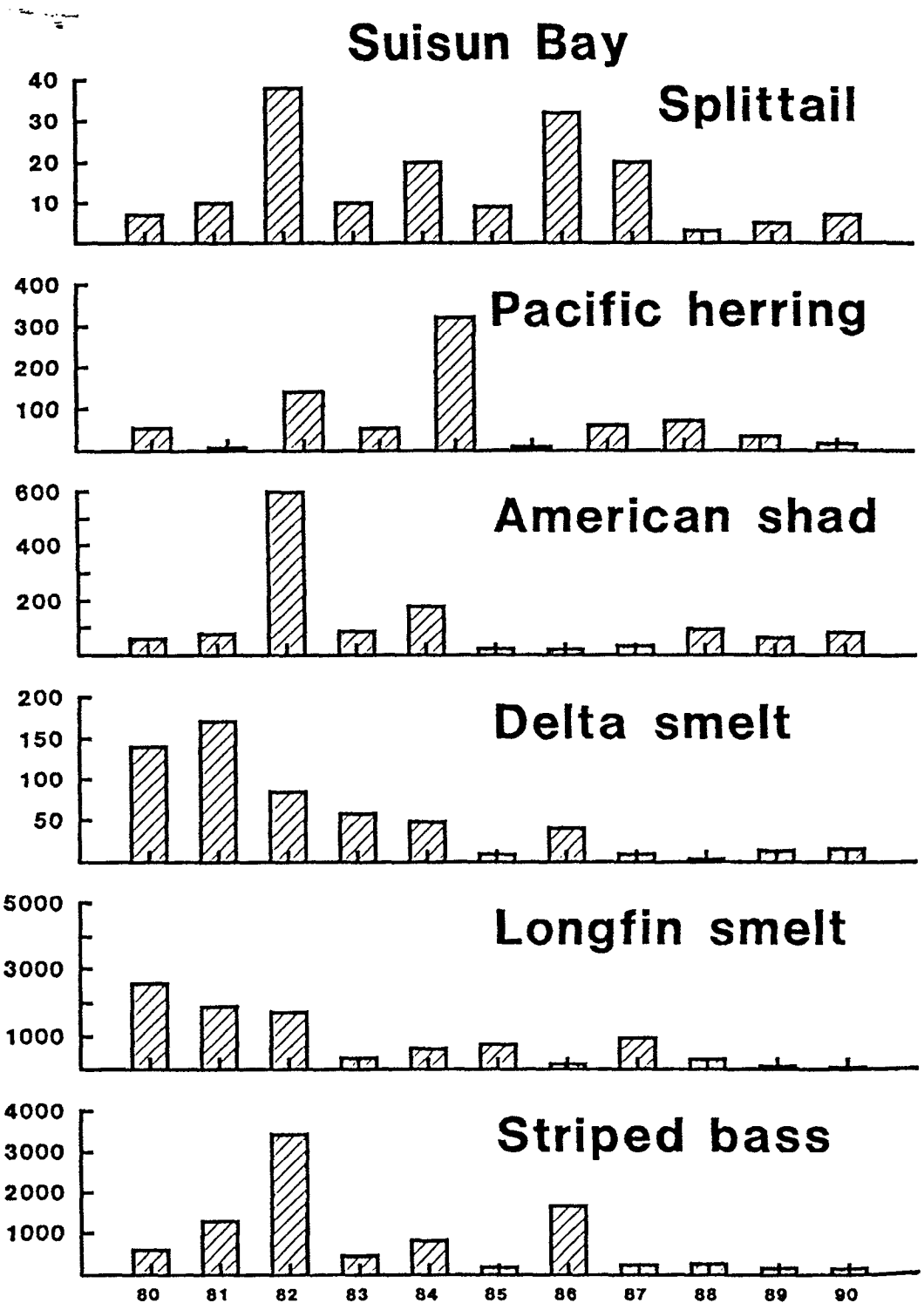


Figure 92. Midwater trawl catches of the bay study for the months of February to August in Suisun Bay.

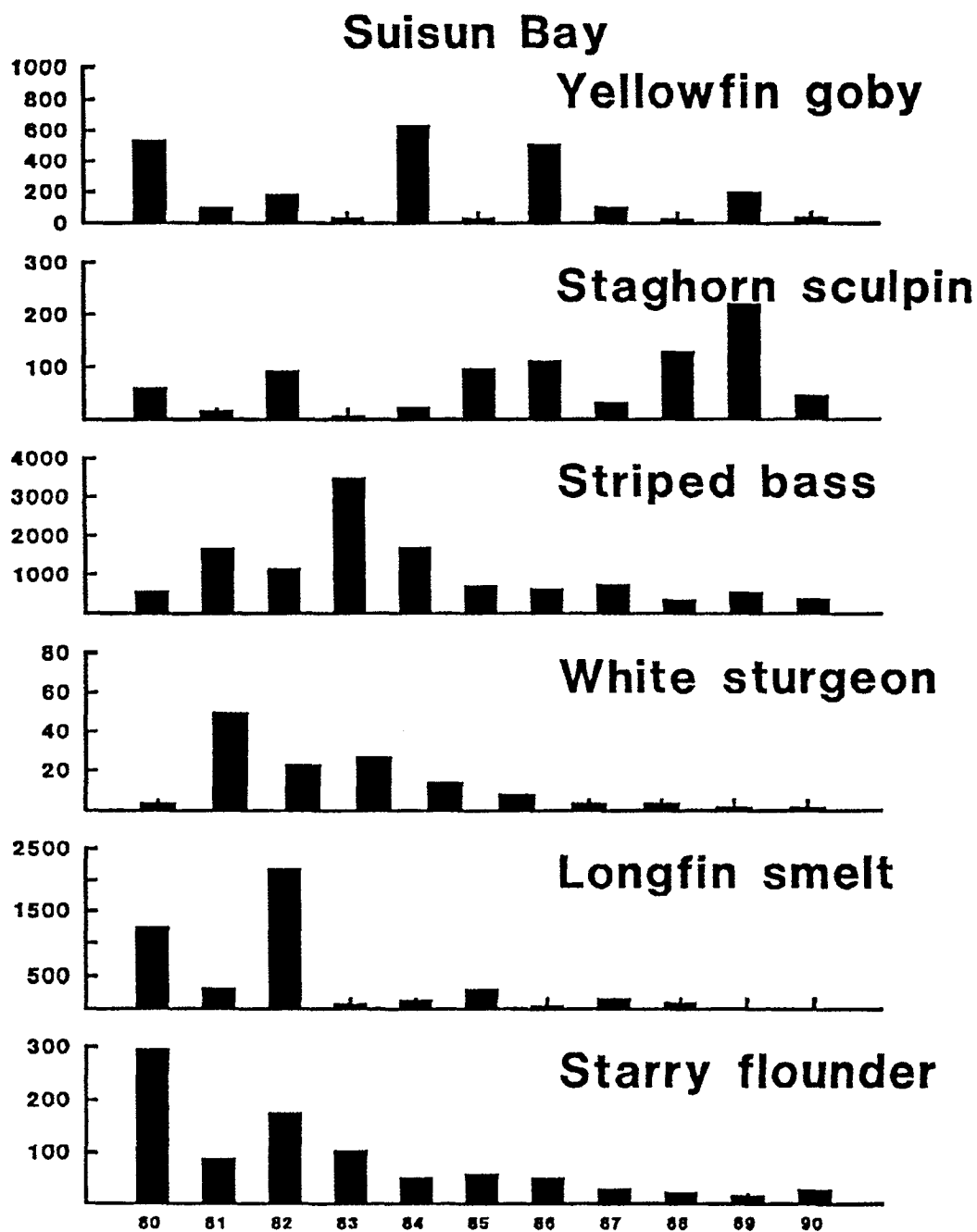


Figure 93. Otter trawl catches of the bay study for the months from February to August in Suisun Bay.

Delta. The stations of the Fall Midwater trawl survey, upstream of Carquinez Straits, reveal a general decline in the freshwater species of the upper estuary (Figure 94). The decline in striped bass has been widely discussed, but similar declines in other species have received little attention. White catfish (*Ameiurus catus*) were one of the most abundant fishes in the first half of the study but they disappeared from the catch following the 1976-1977 drought. The extremely wet year of 1983 was the only time since the earlier drought that white catfish were caught in any abundance. As already described, the other abundant fishes of Suisun Bay and the Delta (American shad, threadfin shad, Delta smelt, and longfin smelt) have all declined since the early 1970s. In the three wet years since 1979 the abundances of striped bass and longfin smelt increased to levels that were common in the first eight years of the study. Fish abundances in normal and dry years are lower than any of the catches in earlier years.

Of the eight most commonly captured species in all three months of the fall midwater trawl, all but American shad and northern anchovy are highly correlated with the passage of time. Striped bass, white catfish, threadfin shad, Delta smelt, and longfin smelt are all negatively correlated; only yellowfin goby is positively correlated (Table 16).

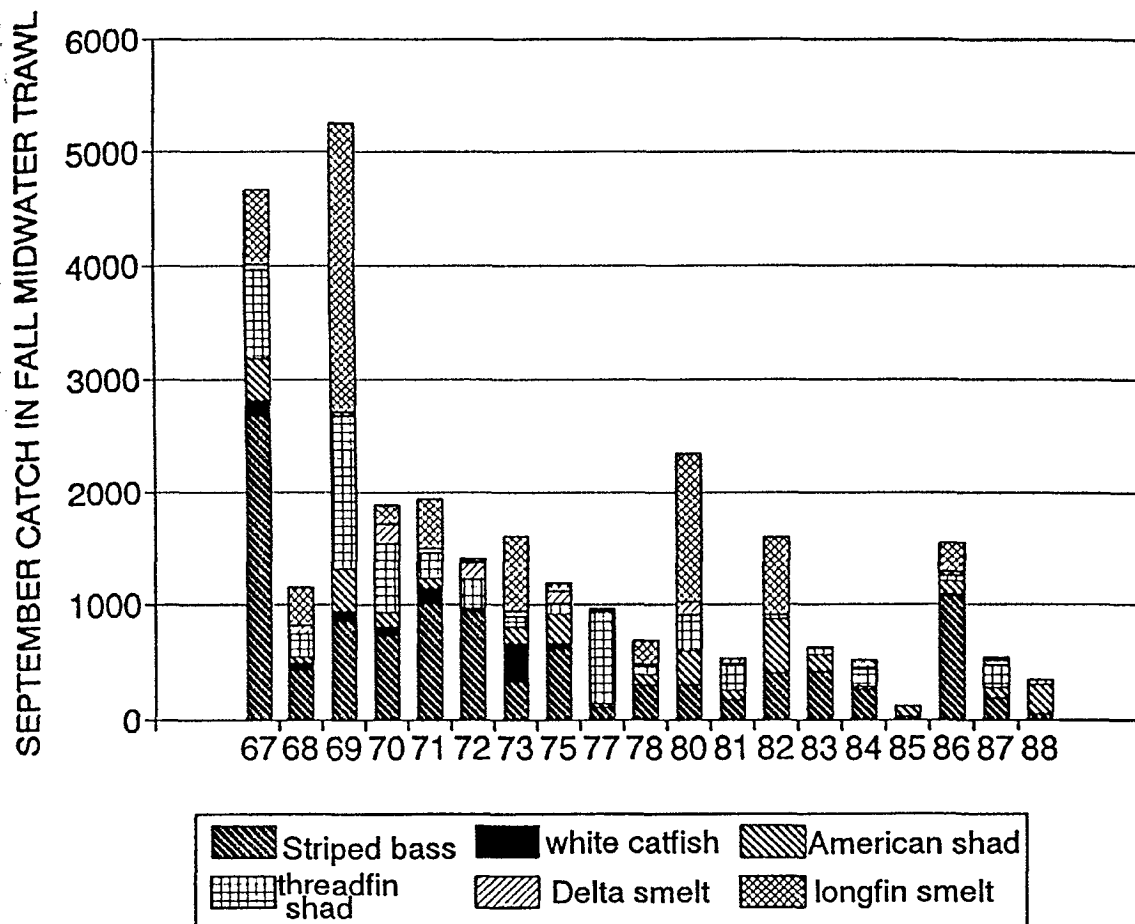


Figure 94. Catch of six most abundant species during September by the fall midwater trawl survey 1967-1988.

Table 16. Correlations of each common species of the fall midwater trawl survey with increasing year 1967-1988 (NS=not significant).

SPECIES	SPEARMAN	PROBABILITY
Striped bass	-.62	< .01
White catfish	-.77	< .01
Threadfin shad	-.66	< .01
Longfin smelt	-.54	< .05
Delta smelt	-.61	< .01
Yellowfin goby	.55	< .05
Northern anchovy	-.10	NS
American shad	-.13	NS

Suisun Marsh. The University of California at Davis sampling program is restricted to a small portion of the estuary but is the only sampling program that encompasses shallow slough habitat. Suisun Marsh contains an wide assortment of native and introduced species, formerly in high abundance. Sampling by Sazaki (1975) found native fishes in the Delta to be concentrated in this sort of shallow habitat, but only in waters of the Sacramento River. In 1979 when the University sampling program began, Suisun Marsh was chosen for study because it appeared to support the densest populations of native freshwater fishes in the estuary.

All of the formerly common species of fish in Suisun Marsh have declined over the course of the sampling program (Figures 95 and 96). Even species of broad ecological tolerances, such as carp and Sacramento sucker, are much less abundant than they were in earlier years. Tule perch are the only species that appear to continue to fluctuate in abundance at abundances similar across the 11 years of sampling. Not included in the graphs, because it only arrived in the marsh in 1987, is the introduced chameleon goby (*Tridentiger trigonocephalus*). This species has increased in abundance from less than .25 per trawl in 1987 to more than 4 per trawl in 1990. Because of the decreased catch of all other species the chameleon goby is often among the three most abundant species in monthly catches.

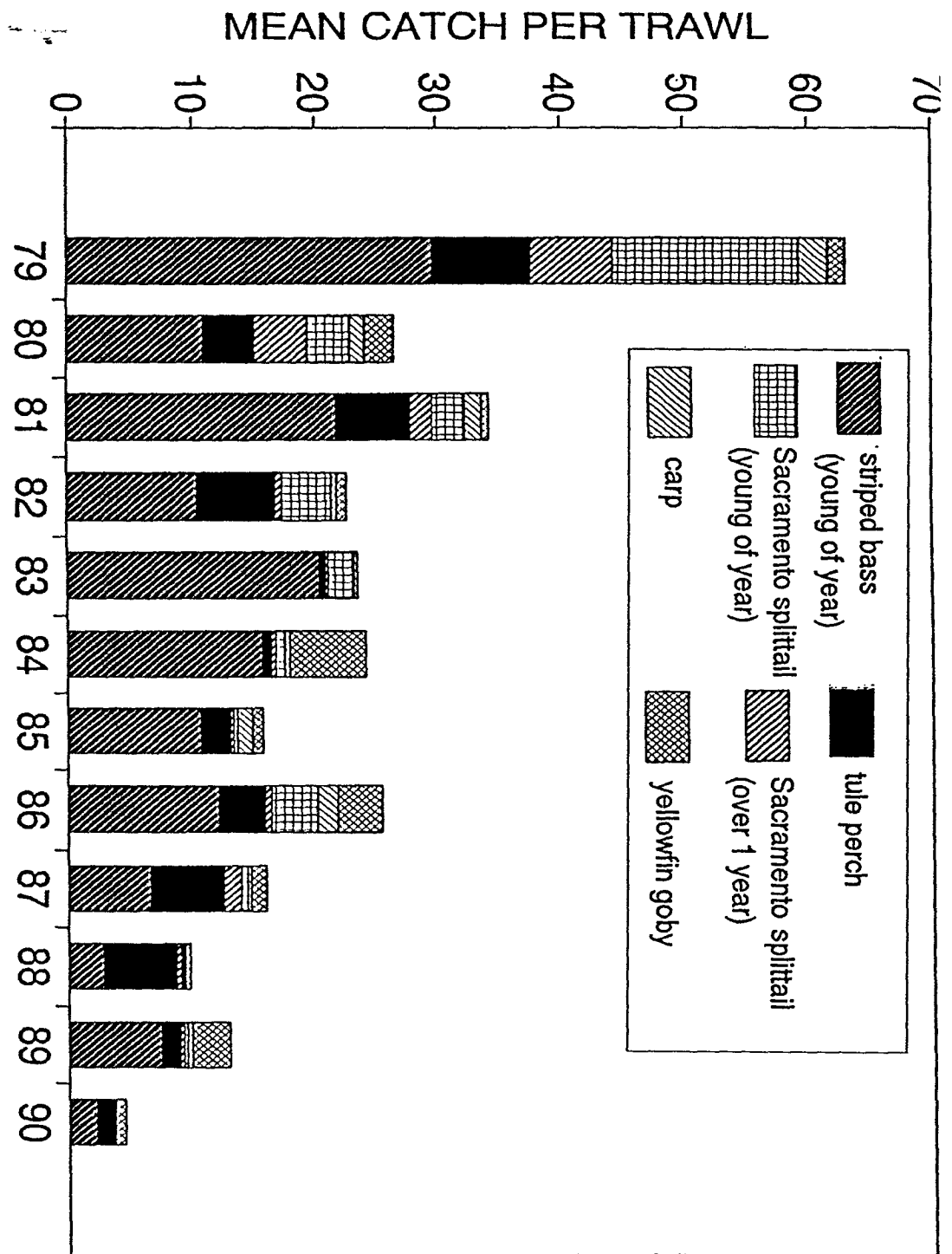


Figure 95 Abundance of six most frequently captured species collected by otter trawl sampling program by UCD in Suisun Marsh.

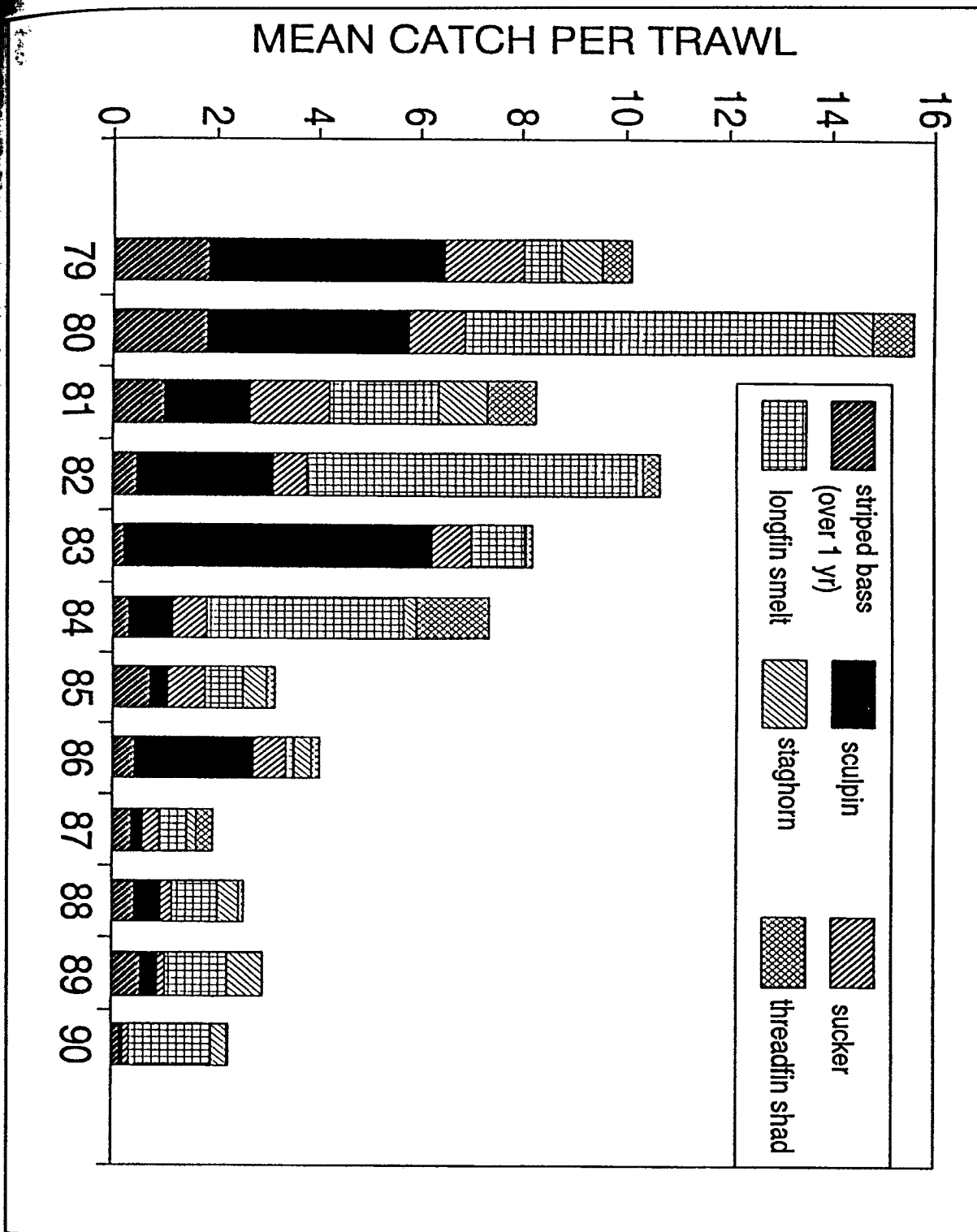


Figure 96 Seventh through twelfth most frequently captured species in sampling of UCD in Suisun Marsh.

5.4.3 Principal components analysis

Principal Components Analysis (PCA) is a mathematical technique to reduce the variability within a dataset by identifying combinations of variables that together account for more variability than single variables. The resulting components may be viewed as combinations of variables which vary together, those with negative signs varying inversely but proportionally to those with positive signs. For example, a PCA of wintertime weather variables such as temperature, precipitation, and barometric pressure in the Bay Area might yield one component that was positive on temperature and precipitation and negative on barometric pressure, another that was positive on precipitation and negative on temperature and pressure. The analyst might then interpret the first component as indicative of tropical storms, the second as indicative of arctic storms. In this analysis we attempt to use PCA to identify oceanic, estuarine and freshwater groups of species and see which are associated with outflow and diversion rates.

In order to identify the species in each embayment that covaried together across years, we used the yearly total for the selected stations. The lack of correlation in abundance of northern anchovy in South and San Pablo bays suggested that other species may also use the two embayments differently. We also wished to identify groupings of species characteristic of different outflow regimes. We, therefore, repeated the analysis including the yearly average for total inflow from the rivers and total exports as calculated from the DAYFLOW data set. Analyses were performed on two measures of species abundance, the total catch for each year and the total number of trawls in which they occurred. These two measures should identify trends within population size and population range. The difference between the two smelts, where one declined in range and the other declined in mean catch led us to seek similar differences in species groups.

Initial analysis of DAYFLOW indicated that almost all interannual variation could be accounted for by total inflow and total exports. Although these two measures were largely independent of each other they were combined in the first principal component in all cases. We therefore present the results of this component as species that increase in abundance when outflows are high and exports are low vs. those which increase under the opposite conditions.

Principal components analysis of the log-transformed data for the eight most abundant species identified two major species associations in each embayment from the Bay Study in both the midwater and otter trawl data (Tables 17 and 18). White croaker, plainfin midshipman, jacksmelt, topsmelt, English sole, and bay goby were frequently grouped together on one component that also associated negatively with flow. Longfin smelt, Delta smelt, striped bass, staghorn sculpin, and starry flounder were often on components in positive association with total river flows. Northern anchovy, shiner perch, yellowfin goby and speckled sanddabs were often on secondary components that did not load heavily on outflow or diversion rates. The analyses were repeated using the frequency of occurrence of each species in the trawl so that abundance and distribution could be compared. Differences

between the two analyses are small and appear to reinforce each other (Detailed tables of these results are presented in Appendix C).

The linkage of most Suisun Bay species with high outflows and low diversions emphasizes the community-wide level of disturbance that the combined effects of climate and water policies of the period since 1984 have produced.

Table 17. First principal components of otter trawls of the Bay Study based on log of abundance associating species with Delta outflow index and total exports of Central Valley Project and State Water Project.

	South Bay	Central Bay	San Pablo	Suisun
higher outflow & lower exports	longfin smelt	longfin smelt English sole	longfin smelt striped bass staghorn sculpin	longfin smelt striped bass starry flounder
lower outflow & higher exports	white croaker plainfin- midshipman	northern anchovy	English sole	none

Table 18. First principal components of midwater trawls of the Bay Study based on log of abundance associating species with Delta outflow index and total exports of Central Valley Project and State Water Project.

	South Bay	Central Bay	San Pablo	Suisun
higher outflow & lower exports	longfin smelt	longfin smelt	longfin smelt	longfin smelt striped bass Delta smelt American shad
lower outflow & higher exports	topsmelt jacksmelt white croaker plainfin- midshipman	white croaker plainfin- midshipman	jacksmelt	none

6 INFORMATION NEEDS

6.1 General overview

Developing an understanding of the estuary as an ecosystem is important to restore the healthy fisheries that the Estuary has supported in the past. Attention to date has largely focussed on particular species or particular areas with little effort to coordinate studies. Development of a general, descriptive model of the aquatic habitats and resources of the Bay and Delta is necessary for coordinated and comprehensive management. To date, species have received attention largely in a crisis management attitude: collapse of fisheries in the Bay was dealt with by removing most commercial fisheries, loss of spawning habitat for salmon was addressed by building hatcheries, massive entrainment of young fish by diversions is avoided by trucking hatchery salmon further downstream and by supporting commercial hatcheries for striped bass. The declines of numerous species that depend on the Delta and Suisun Bay habitats should provide convincing evidence that there is a general environmental problem rather than a series of species-specific problems. Solving the problem from a unified and scientific approach is likely to be more effective and efficient than a piecemeal approach.

In order to attain a useful understanding of the estuarine ecosystem several steps are needed:

1. Determine patterns of use for the major species of each embayment, regardless of their *prima facie* economic value. For example, northern anchovies are the most abundant fish in the Bay but it is unclear to what extent they actually spawn in the Bay, how much of their feeding represents a loss of food for other fishes, or how much of the anchovy population that enters the Bay represents productivity from the ocean that becomes food for animals in the Bay.
2. Determine the productivity of the various parts of the estuary and identify where the food for aquatic animals comes from. The movement of food materials among areas is an essential part of the determination of productivity possible by animals in each area. Appendix A represents a first effort toward answering this problem and illustrates the value of a community approach. Suisun Bay has been described as an important nursery area because of the presumed high productivity there. If this is the case, and the nursery value of Suisun Bay rests on food inputs from river flow, then no manipulation of salinity or flow pattern within Suisun Bay can compensate for reduced river outflow.
3. Determine the trophic connections of the aquatic resources of the Bay. Knowing the amount of food that is available generally is insufficient to estimate the production of higher trophic levels unless the energetics of the trophic system are known. Food habits of the animals of the Sacramento-San Joaquin Estuary are poorly known so that the abundance and distribution of lower trophic levels provides little information on the production of higher levels. Production of *Melosira*, *Sinocalanus*, or *Potamocorbula* is unlikely to provide the same fish abundances as equivalent densities of *Asterionella* or *Eurytemora*. Simply determining the number of trophic levels would provide a much more sound basis for estimating potential fish production.

4. Identify the sources of mortality and mortality rates for representative species in each habitat. Focussing research on a long-lived species like striped bass has permitted short-lived species to approach extinction. Sensitive species could provide an effective early-warning system for disruptions to the environment of the Bay and Delta, rather than simply being the species most apt to become extinct.

5. Develop an understanding of how introduced species invade the estuary and establish populations in order to improve our abilities for prevention and control of unwanted exotics.

Developing this sort of ecological understanding of the estuary before more species go extinct requires more work than can reasonably be expected by agencies under the present budgetary restrictions.

Recent coordination of effort of university researchers with agency researchers has yielded answers to significant questions regarding the feeding success, dietary habits, and physiological stresses in striped bass and new information on the breeding biology of the threatened Delta smelt. The increased involvement of the academic community has been due partly to an active program by state agencies to encourage them. The Interagency Ecological Studies Program and the San Francisco Estuary Project initiated the University Academic Research Involvement Program which should help increase university interest in the Estuarine Studies of the Sacramento-San Joaquin Estuary lag behind the work in Atlantic estuaries where there has been a long and fruitful history of cooperation among agency and university personnel.

6.2 Productivity

Phytoplankton productivity. Changes in the array of sampling stations are warranted. Three issues in particular need to be addressed. First, primary productivity in shoal areas dominates that in deeper areas, especially in Suisun Bay, yet most data are collected from channel stations. Second, almost no long-term series of chlorophyll or productivity measurements are available for Central and San Pablo bays. Little is known, consequently, about the entrainment zone when it is pushed out of Suisun Bay by high flows. Third, certain areas in South and Suisun bays appear to be oversampled in space, relatively speaking. In the South Bay, for example, the region between San Bruno Shoal and the Dumbarton Bridge exhibits much less spatial variability than the region between the Golden Gate Bridge and San Bruno Shoal. A similar analysis of data landward of the Carquinez Strait reveals tight clusters of stations, such as from Chipps Island to Point Sacramento.

Time series for the Bay are thus characterized by periods with relatively high frequency data, and regions with relatively high-resolution data, interspersed with long gaps in time and space. The irregularity in sampling hinders the potential value of the data that are collected particularly for understanding the long-term changes that may now be underway globally. A commitment needs to be made to a group of "index stations" that will be sampled at a regular frequency for at least chlorophyll *a* and extinction coefficient (or, equivalently, phytoplankton biomass).

depth) into the indefinite future. Some of the current effort in the channels should be shifted to shoal sites. Similarly, some of the current efforts in South and Suisun bays should be shifted to Central and San Pablo bays. If this basic, "index station" program is made as simple as possible, its longevity would be more likely. The number of stations and the sampling frequency should therefore be as modest as possible. The abundance and distribution of benthic organisms should be carefully considered in choosing index stations, as the benthos provide a kind of "integrated moving-average" indication of chemical and planktonic conditions.

Actual primary productivity measurements are not necessary, as productivity can be deduced from biomass, turbidity, and light availability. But given the importance of light availability, a permanent station should be established for measuring surface irradiance. The absence of continuous, reliable, irradiance measurements hinders the interpretation of existing data sets.

Assumptions about aphotic respiration have a large effect on estimated productivity, particularly in Suisun Bay. Yet little direct evidence exists on the magnitude of these respiratory losses. Further experimental work on aphotic respiration in San Francisco Bay would be a definite contribution, particularly work that would improve estimates of net water column productivity.

Benthic microalgal productivity. No measurements have yet been made on benthic microalgal productivity, despite their possible significance, especially in South and Central bays. As discussed previously, prevailing measurement techniques may be unreliable. Although suitable methods may not be available for San Francisco Bay, this issue does require more attention. At the very least, sampling of sediment chlorophyll could accompany water column measurements at index stations. The product of sediment chlorophyll and light incident on the sediments could serve as a relative index of benthic productivity. Incident light could be estimated from measurements of surface irradiance and extinction coefficient (photoc depth) at the sampling stations.

Delta discharge. Delta discharge may be the largest source of organic matter for Suisun Bay and is probably a significant one for the northern reach as a whole. The load of organic carbon to San Francisco Bay from the Delta needs to be measured on a regular basis. Due attention needs to be given to POC as well as DOC, and to bottom samples as well as near-surface samples. Because of the probable episodic nature of organic carbon loading, sampling must be able to resolve the succession of storms that characterize the winter period. Because of the apparent importance of riverine algae, chlorophyll and derived pigments also should be measured in tandem with organic carbon.

The issue of availability needs to be addressed as well. BOD measurement offers one perspective on this problem. Ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.) need to be continued and extended. Additional approaches also must be sought.

Tidal marsh export. Tidal marsh sources may be of importance for Suisun Bay, particularly during drought periods. Direct estimates of tidal marsh export are virtually impossible, in part because of the difficulty in determining residual flows from tidal exchange. The uncertain availability of exported organic carbon is another obstacle. Hence, indirect methods are required to address this question. The use of multiple stable isotope markers appears to be of value. B.J. Peterson et al. (1985), for example, using ^{13}C , ^{15}N , and ^{34}S , was able to show that benthic macroinvertebrates consumed *Spartina* detritus and plankton in preference to terrestrial plant detritus. A similar study in Suisun Bay may be able to determine at least the qualitative significance of tidal marsh export.

In view of the large export of reduced sulfur encountered for some marshes (Peterson et al. 1980), a preliminary investigation of sulfide oxidation activity related to tidal marsh exports is warranted.

6.3 Circulation and mixing.

The system boundaries need to be considered carefully in relation to physical transport. At the minimum, transport through the Golden Gate requires definition and should be the first objective. A carbon budget for the entire Bay would then be feasible.

Further subdivision needs to be done carefully, with due regard to topographical features and the existing data. As implied in the previous discussion, the segmentation scheme normally used landward of the Golden Gate requires some revision. The boundary between South and Central bays, in particular, perhaps should be shifted to the San Bruno Shoal. The northern extent of "Central Bay," currently at Point San Pedro-Point San Pablo, also requires re-examination from a hydrodynamic point of view. In addition, the utility of the boundary between San Pablo and Suisun bays needs to be addressed. The entrapment zone, as well as organic matter from riverine loading, moves freely across the boundary as flows increase. From the point of view of establishing subregions for a carbon budget and subsequent food web analysis, the distinction between the two subembayments may have little value. On the other hand, a further subdivision of South Bay at the Dumbarton Bridge appears warranted in view of the higher point-source loading, relative tidal marsh area, and runoff south of the bridge. A lack of primary productivity measurements in lower South Bay would be an impediment to this subdivision, which is something to be considered also in the choice of index stations (see above).

Whatever the boundaries, direct measurements of transport are an unrealistic goal, for the same reason that tidal marsh export cannot be assessed with any accuracy. But the flow field can be characterized from existing data and modeling studies. In principle, the flow data can be combined with concentration data for various organic matter fractions to estimate transport across the major boundaries. In practice, the concentration data do not appear to be adequate in many locations. Modeling studies, therefore, must be accompanied by a supplemental field measurement program for organic matter fractions, particularly DOC, various size fractions of POC, and chlorophyll. At the minimum, measurements are needed at the Golden Gate.

Gate, including horizontal gradients through the Gate and vertical profiles both seaward and landward of the Gate.

6.4 Food web structure.

The structure of the food web connecting organic carbon sources to higher organisms is critical in determining the magnitude of their food supply. The number of trophic linkages, for example, is especially important in controlling the efficiency of energy transfer from sources to macroscopic consumers: If energy is transferred with an average efficiency of, say, 10% along each link, then the interposition of an intermediary organism has the same effect as a ten-fold drop in the food supply at the base of the food web.

At the macroscopic level, food webs have been delineated in a number of ecosystems, as recently reviewed by Schoener (1989). At the microscopic level, on the other hand, the relative importance of many postulated pathways has not yet been demonstrated (Mann 1988), for the Bay or for other ecosystems. In view of the nature and number of these microscopic interactions -- involving autotrophs, DOC, bacteria, protozoans and small metazoans -- a complete characterization of the Bay's food web appears to be an unrealistic goal for the near future.

It is possible, nevertheless, that a complete characterization is unnecessary. Circumstantial evidence from other ecosystems suggests that the major pathways through the food web are sometimes relatively simple. Demersal fish production, for example, often has a high efficiency when compared to organic carbon sources for the benthos (reviewed by Mann 1982). Energetic considerations require that settling organic matter be consumed directly by macrofauna and passed to demersal fish in order to account for this high efficiency. If the other components of the benthos do, indeed, have a secondary role, then the current lack of quantitative knowledge regarding bacteria, microfauna, and meiofauna in San Francisco Bay sediments (Nichols and Pamatmat 1988) may not be a major impediment. Note, however, that the "small food web" consisting of micro- and meiofauna does compete for food with the macrobenthos of some estuaries (e.g., Wadden Sea; Kuipers et al. 1981).

A comparison of benthic macroinvertebrate productivity (e.g., Nichols 1977) with primary productivity would be especially pertinent, particularly during bloom periods when most of the annual phytoplankton production takes place. If macroinvertebrate productivity were a high enough percentage of microalgal productivity, then a direct link from primary producers to the large benthic invertebrates would be implicated. Lower percentages would imply either that intermediate consumers were present in the water column or sediments, or that the planktonic food web was a significant sink for organic matter. A related study in the South Bay is currently in the initial planning stages (J. Thompson 1990, pers. comm.). A similar investigation is warranted for Suisun Bay. The results of these studies, combined with

ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.) should provide a guide for further research within the benthic habitat.

Even though the major pathway *within* the benthic habitat may be simple, organic matter from primary productivity may undergo transformations *before* coming into contact with the benthos. For instance, the close relationship in San Francisco Bay between bacterial activity and biomass, on the one hand, and phytoplankton productivity, on the other (T. Hollibaugh 1990, pers. comm.) points to a "microbial loop" (Azam et al. 1983) in this estuary. Bacterial processes also may play an essential intermediary role between allochthonous sources of organic matter and larger planktonic or benthic invertebrates. Riverine phytoplankton, for example, must undergo osmotic stress within the vicinity of the entrainment zone, probably liberating organic material for bacterial processing. Also, detrital material from upstream may be colonized by bacteria and rendered more desirable and nutritious for consumers such as *Neomysis mercedis*, which often has abundant detritus in the gut (Kost and Knight 1975). The number of trophic links in the water column may radically affect the food supply to midwater fish and the benthic habitat, whether these links occur on a microscopic or macroscopic level. A continued investigation into planktonic microbial processes is therefore warranted. The detailed study of mechanism, however, should be accompanied by attempts to determine whether a simple pathway dominates. As in the case of the benthos, simultaneous measurement of both organic matter sources and production of the larger planktonic invertebrates may provide the necessary clarification. These measurements would be most informative if done in conjunction with those for the benthos.

The pathway of energy through the Estuary's food web is largely conjectural, except for a few well-studied species and small areas. Meioplankton (rotifers, protozoa, etc.) have been almost completely unexamined, but as an additional trophic level, they could represent a major reduction in the amount of fixed carbon that is available to higher trophic levels.

Trophic studies of aquatic resources in San Francisco Bay and Delta have focussed almost entirely on striped bass, which show strong seasonal and age shifts in food habits. There is no reason not to expect similar complexity in the dietary habits of many other species. Without such knowledge, the effects of changes in productivity on higher trophic levels is very loose conjecture.

The emphasis of research on an introduced, hardy, and fecund fish like striped bass has delayed recognition of the status of several native species. Secondarily, the emphasis on striped bass has limited the scope of subsidiary studies to a restricted geographic part of the estuary. Studies based on more sensitive species, on species representing a diversity of habitats within the estuary and on species of diverse trophic patterns would allow a much more accurate and sensitive monitoring of conditions. Thus, perhaps we could develop an ecological understanding that would allow us to progress past the pattern of emphasizing a single species that has characterized the management of sardines, salmon, and striped bass.

7.5 Sampling procedures and programs

Zooplankton studies of the estuary have been largely concerned with documenting the food chain affecting striped bass. Consequently, zooplankton data for Central and South bays are extremely sparse. Because food webs in these embayments probably rest on autochthonous production, an understanding of the role in consumption played by the abundant seasonal species (particularly northern anchovy) is crucial to determining the amount of energy available as food for resident species.

The absence prior to 1980 of any regular, year-round sampling of fishes in most of the estuary has severely restricted the possible analyses of status and trends. Without a regular sampling program for the benthos, zooplankton, and fishes throughout the estuary, the effects of water policy changes, climatic shifts, and species introductions will remain a confused mix of suspected causes and observed effects. Underfunding of the DFG Bay Study in 1989 and 1990 led to cessation of sampling for some months at a time when several species were showing the effects of extended periods of low river outflow. Similar interruptions in other sampling program during an earlier drought probably deprived us of information that may have been important in understanding the effects of drought on fishes. The commitment of adequate funds to these programs, and the personnel necessary to run them, is of the greatest importance in protecting and understanding the resources of the Bay.

7.6 Life history and habitat requirements

In 1966 (Kelley 1966; Turner and Kelley 1966) a description of the fishes and invertebrates of the Estuary covered the distribution, abundances, and life history of most of the dominant species. The importance of dead-end sloughs, both in terms of their high concentrations of food and as principal habitat for many species was suggested by preliminary surveys. The importance of these habitats to several species was further emphasized in surveys conducted by Sazaki (1975). Since then several excellent reviews of biological work done in the Estuary have appeared (e.g. Conomos 1979, Cloern and Nichols 1985, and Nichols et al. 1986, as well as many reports to the State Water Resources Control Board). However, in looking at how to protect Delta smelt from extinction it has become clear that we have too little knowledge to be able to identify spawning areas or habitat requirements for any of the fishes that use shallow channels in the Delta. Identification of the critical habitat of this species will have to encompass a larger region than is perhaps necessary in order to be sure of adequate protection. A number of other species which also probably rely on shallow Delta habitats for spawning may also be headed for the listing process (such as longfin smelt and Sacramento splittail). Sampling programs are needed to determine specific habitat requirements of native fishes and other organisms and the extent to which the species of the Delta can be managed as a community.

7.7 Tributary streams

Tributary streams to the Bay are isolated fragments of habitats that support or have supported 10 of the 17 fish species endemic to the Central Valley as well as populations of several listed species, including the freshwater shrimp (*Syncaris pacifica*). These streams also support remnant populations of steelhead, chinook salmon and coho salmon. Although these streams are significant reservoirs of California's biodiversity, they have been the subject of little research but major habitat alteration (Leidy 1984). Surveys are needed to identify which streams are still home to these heritage resources, how they might be preserved, and their importance as organic carbon contributors or as spawning habitat for species of the Bay.

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Appendix A

Organic carbon sources for the food web of San Francisco Bay

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SUMMARY

The sources of food and energy for estuarine food webs are diverse. These sources include primary production within the estuary (autochthonous sources); organic materials flowing into the estuary from the rivers, land, and atmosphere (allochthonous sources); and exchange with the ocean (transport sources; Fig. A.1). The first step in assessing food availability to higher organisms in the Bay is a systematic accounting of these sources. They are usually measured in the common currency of "organic carbon" content.

The Bay was divided into South, Central, San Pablo, and Suisun bays for assessing organic carbon sources. Hypsographs and related morphometric data were assembled for each subembayment (Table A.2, Fig. A.2).

Estimates were made of each organic carbon source for each subembayment using a variety of techniques. Phytoplankton productivity was estimated from a morphometric model and measurements made in 1980 (Table A.3, Fig. A.3). Benthic microalgal productivity, seagrass productivity, and tidal marsh export were estimated from habitat area in conjunction with the range of values (on the basis of unit area) published for other estuaries. Delta discharge, point sources, nonpoint source runoff, atmospheric deposition, spills, and dredging sources were all estimated from data collected for San Francisco Bay. Macroalgal productivity, photosynthetic bacterial productivity, groundwater contributions, and biotic transport could not be estimated quantitatively, but were assessed on the basis of qualitative considerations. Transport due to circulation and mixing could not be estimated.

The available data permitted a comparison of the different carbon sources for 1980. Phytoplankton productivity, benthic microalgal productivity, and Delta discharge of organic matter probably were major sources ($>25\%$) for at least one subembayment. Tidal marsh export, point sources, and dredging transport probably were significant secondary sources ($>10\%$) for at least one subembayment, but never major sources. Seagrasses, macroalgae, photosynthetic bacteria, runoff, atmospheric deposition, spills, groundwater, and biotic transport appear to have been minor sources ($<10\%$ total), regardless of subembayment.

For San Francisco Bay as a whole, phytoplankton productivity was the dominant and only major source (50%), and benthic microalgal productivity was the only significant secondary source (20%). All other sources contributed less than 10% of the total. Comparisons for the whole Bay, as well as for each subembayment, assume that only about one-tenth of Delta discharge was actually available to the food web.

For South Bay, phytoplankton productivity was the dominant source (60%) in 1980, but benthic primary productivity was probably a major source (30%) as well.

Since 1980, annual phytoplankton productivity in the photic zone of the channel fluctuated within a factor of two, but no long-term trend can be observed. Productivity tends to increase with annual Delta discharge, apparently because higher Delta outflow promotes stratification of South Bay waters. Stratification, in turn, leads to higher growth rates and lower losses to suspension-feeding benthic macroinvertebrates. Productivity may remain low as long as Delta outflow is depressed. The lack of long-term data on shoal phytoplankton (accounting for 60% of total phytoplankton productivity) and benthic microalgae prevents more certain conclusions.

7. Phytoplankton productivity (40%) and benthic microalgal productivity (30%) appear to have been the major sources of organic carbon for Central Bay in 1980. Point source loading (10%) and transport of dredging spoils from adjacent subembayments (10%) could have been significant secondary sources.

Insufficient data exist to characterize interannual variability of phytoplankton or benthic microalgae since 1980. The available evidence suggests that mechanisms for phytoplankton variability in Central Bay are different from those in South and San Pablo Bay, including possibly a major influence from the coastal ocean. Point source loading continued to decline after 1980. Dredging exhibits much interannual variability, but with no trend.

The usual boundary separating South Bay from the central basin for analytical purposes needs to be reconsidered.

8. San Pablo Bay was dominated by phytoplankton productivity (60%) in 1980. Benthic microalgal productivity (20%) and marsh export (20%) may have been significant secondary sources of organic carbon.

No long-term data exist for shoal phytoplankton, which accounted for almost 80% of the estimated phytoplankton productivity. However, the mechanisms controlling interannual variability in San Pablo Bay are thought to be similar to those in Suisun Bay.

9. The dominant organic carbon source for Suisun Bay probably was riverine loading from the Delta (60%) in 1980, even when only one-tenth is considered available as food. Marsh export (20%) and phytoplankton productivity (10%) may have had a secondary role. Much of the organic matter contributed in Delta discharge seems to have been phytoplankton and its breakdown products.

The current drought period that began in 1987 is a time of depressed Delta outflow and presumably, depressed riverine loading of organic matter. Phytoplankton productivity also has been low since 1983. The low phytoplankton productivity has been attributed to two mechanisms. First, the entrapment zone, which retards advective losses of phytoplankton from its vicinity, is absent during periods of extremely high or low Delta outflow. Second, suspension-feeding estuarine invertebrates become established during periods of prolonged

drought and are responsible for increased grazing losses. Tidal marsh export could actually be a major organic carbon source at present.

The invasion of the corbulid clam *Potamocorbula amurensis* in 1987 may lead to the persistence of high grazing losses even after the drought ends, due the clam's tolerance for freshwater conditions. If so, autochthonous productivity could remain low and riverine loading (and tidal marsh export) would be even more important as an organic carbon source.

Evidence from hydraulic residence times, benthic invertebrate consumption rates, and oxygen consumption suggests that most organic carbon sources in the South Bay enter the food web. The same can be said for the northern reach as a whole. On the other hand, organic carbon sources for Suisun Bay -- particularly riverine loading -- may actually be consumed downstream in San Pablo or upper Central Bay.

Based on empirical generalizations from a synthesis of work at other estuaries, as well as the apparent importance of food supply for zooplankton in Suisun Bay, a decline of total fish production in San Francisco Bay -- particularly the northern reach -- could have accompanied the decline of organic carbon sources since the early 1980s. The applicability of these empirical generalizations, however, is uncertain for San Francisco Bay. Further, conclusions can only be made about the relation between organic carbon sources and *total* fish production, not the production of any one population, on the basis of these generalizations.

During drought conditions, relatively more of the organic carbon supply may be shunted through benthic, rather than planktonic, pathways, favoring a relative increase in demersal fish.

Suggestions were made for future monitoring and research programs regarding phytoplankton and benthic microalgal productivity; Delta outflow of organic materials; tidal marsh export; circulation and mixing; and food web structure.

A.1 INTRODUCTION

A.1.1 Significance of organic carbon budgets

The sources of food and energy for organisms at the base of estuarine food webs are diverse compared to those of other ecosystems. This diversity arises from several features characteristic of estuaries. Tidal fluctuations create intertidal habitat for benthic micro- and macroalgae, and marsh for higher plants. Rivers carry in food materials from upstream, as well as inorganic nutrients to support photosynthesis by phytoplankton and other primary producers within the estuary. Finally, sewage and other waste products of nearby human communities are often a source of food for microbial populations and, ultimately, for the food web supporting higher organisms.

Because characteristics such as morphometry, river discharge, and human population densities differ so much from one estuary to another, the exact mix of potential food sources is unique to each estuarine system. Because of this diversity and uniqueness, it is not possible to understand the existence of or potential for food limitation of higher organisms -- the larger invertebrates, fish, sea mammals, and birds -- without first undertaking an explicit accounting of the types and amounts of food entering at the base of the food web.

If the various food sources are to be compared, they must be expressed in terms of a common currency. Organic carbon units rather than energy units are used here, as the former is more often measured on field samples. In practice, one usually describes food sources in units of either organic carbon or energy simply because the information rarely exists to undertake a more sophisticated characterization. The ramifications of this simplification must be kept in mind, however. Food acts as a source of structural material and energy, but it also provides specialized molecules (e.g., vitamins); the actual food value of a substance cannot be fully characterized in a single dimension. The mere fact that a substance contains reduced carbon does not mean that it can be ingested or assimilated by organisms. By virtue of size, shape or chemical composition, food materials may be partially or entirely unavailable to consumers. For most food sources, however, there is little information on availability to primary consumers and the organic carbon or energy values must be accepted at face value. This issue is particularly relevant to the interpretation of river-borne organic carbon and we return to it later in connection with Delta discharge.

The "accounting" of various food web pools and fluxes in terms of organic carbon is usually referred to as a "carbon budget." Carbon budgets can assume various levels of detail. The most basic budget, which we shall examine here, consists of all sources and sinks for the organic carbon pool as a whole -- in other words, a one-compartment model -- considered on an annual basis. The internal dynamics of the organic carbon pool are not treated at all at this stage, nor are the total organic carbon (TOC) fluxes fractionated into such categories as dissolved organic carbon (DOC) and particulate organic carbon (POC). These further refinements, if found to be desirable -- and possible -- can be constructed on the basic carbon

budget as a foundation. The effort necessary to provide other than a basic budget does not conform at all to the time constraints of the current report. In addition, an adequate treatment of the Delta could not be accomplished for this report, which is therefore confined to San Francisco Bay. It was believed preferable to accomplish at least part of the task as well as the data permitted, rather than to provide more superficial but broader spatial coverage. The current treatment, despite its brevity and inadequacies, at least can serve to motivate and orient the ongoing analysis aimed at greater accuracy, more spatial coverage, and finer resolution in both space and time.

The basic budget does include all sources of organic carbon arising within the estuary ("autochthonous" sources), as well as organic carbon which is transported into the estuary ("allochthonous" sources). These sources must balance sinks of organic carbon within the estuary plus transport of organic carbon from the estuary. As our goal here is to clarify the nature of energy flow *into* the food web, sinks or losses from the organic carbon pool will not be treated explicitly. When sink terms can be completely characterized, they are of value in solving mass balance equations for the magnitude of certain sources that cannot otherwise be quantified. In the case of the San Francisco estuary, however, the uncertainty in source and sink magnitudes precludes such an approach.

Not all processes can be characterized a priori as either a source or a sink. For example, tidal exchange can potentially act as either, depending on the gradient of carbon across the mouth of the estuary and other factors. It seems most useful, at the beginning, to classify processes according to whether they are definitely a source, definitely a sink, or have the capacity to be either a source or sink, depending on the circumstances. The first two kinds can be thought of as "unidirectional" processes, the last kind as "bidirectional" or perhaps "exchange" processes of unknown net sign. Note that exchange processes may be biotically mediated -- for example, fish migration into or out of the estuary -- as well as due to physical processes.

Many processes of potential importance can be specified (Fig. A.1). Some of these turn out to be clearly of importance in the San Francisco estuarine system, others clearly negligible. Still others -- perhaps the majority -- cannot yet be established with any useful accuracy. Despite the large amount of good research that has been accomplished in the estuary, development of a carbon budget has never been an explicit goal. As a result, we understand certain processes in detail (e.g., phytoplankton production) and others not at all (e.g., benthic microalgal production). The present undertaking cannot remedy this problem. But by making these gaps in our understanding explicit, the current endeavor can summarize existing knowledge systematically and contribute to a rational approach for orienting further research. In particular, we seek to answer a certain sequence of questions: What organic carbon sources can be identified as clearly important components of the total flux into the organic carbon pool? What sources might be important? What sources are probably negligible? In this manner, the basic carbon budget and its refinements can serve as a useful conceptual framework for understanding the dynamics of the San Francisco estuary, as it has for many other estuaries.

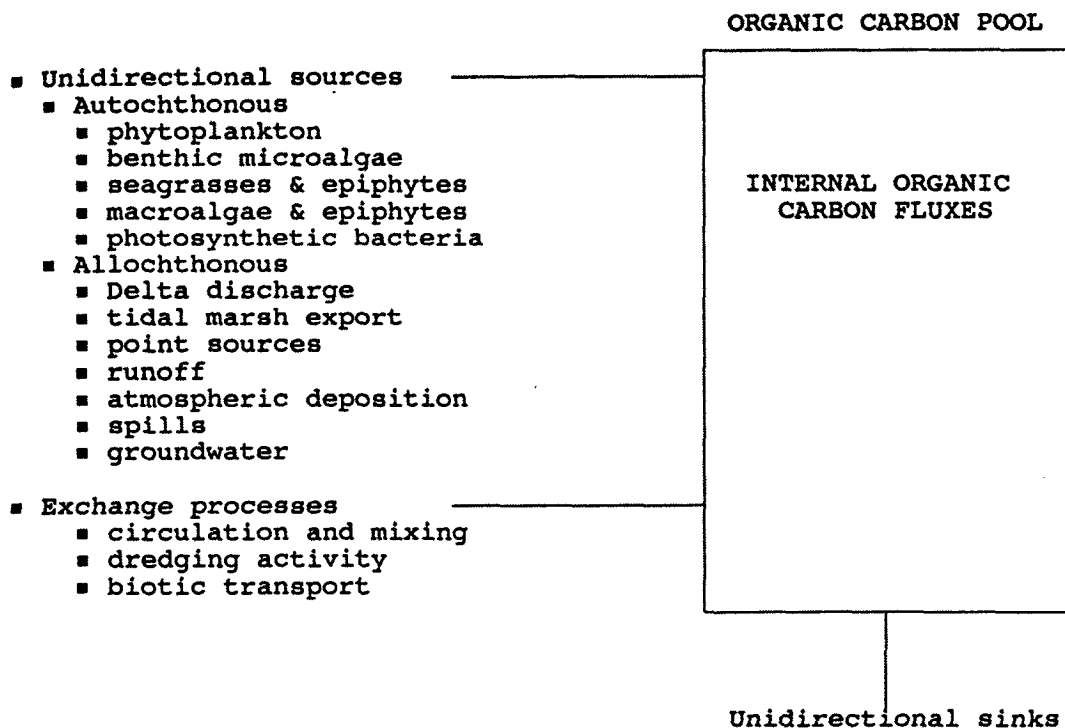


Figure A.1 Sources for the San Francisco Bay organic carbon pool.

The annual carbon budget itself is a function of time, not a collection of static quantities. Many of the fluxes contributing to the budget must change from one year to the next, and their relative importance thus may change as well. Unfortunately, estimates for each flux are available only for one or a few years, often not overlapping. In view of the lack of data, it seems pointless to attempt an explicit budget for each individual year. Nevertheless, as many fluxes that appear to dominate the carbon budget were in fact measured during 1980, a year of "intermediate" Delta outflow, we eventually use 1980 as a reference point and attempt a budget for that year. Using this budget and various other considerations, we try to delineate those processes that were probably negligible both in 1980 and subsequent years, even in the face of strong year-to-year variability. For the remaining processes, the following questions are also addressed: What interannual changes can be identified, and what were the underlying reasons? What do these causal mechanisms imply about these fluxes since 1980 and in the coming years?

In addition to "best estimates" for each carbon source, an attempt will be made to arrive at an *uncertainty range*. It will be assumed in some cases that the possible values can be approximately described by a normal distribution; the estimate will be set equal to the mean and the uncertainty range will be set equal to the 95% CL. A true normal distribution is actually impossible in many of these cases, such as when a flux is physically constrained to be nonnegative. For other carbon sources, both the estimate and the uncertainty range will be based on the range of literature values, but with no assumption of an underlying distribution. The estimate need not necessarily be at the midpoint of the range. The choice of estimates and

uncertainty ranges obviously has a subjective component that could lead to error. For many poorly-studied processes, for example, future measurements may be found to lie outside the range. Erring in the other direction, certain values reported in the literature may represent extreme situations that result in an unnecessarily large uncertainty range for San Francisco Bay. Despite the approximate nature of these ranges, they serve to caution the reader regarding the validity of "best estimates" of carbon flux. Furthermore, despite the large sizes of many of the uncertainty ranges, deductions are still possible concerning the relative importance of different carbon sources.

All estimates are rounded off to at most 2 digits. The second digit is retained to prevent roundoff errors in the first digit, but probably only one digit is significant. When a value is reported in the form $x \pm s$, x refers to the mean but s may refer to the standard deviation (SD), standard error (SE), or 95% confidence limits (95% CL); the exact meaning will be stated.

A.1.2 Morphometric considerations

In constructing a carbon budget, it is first necessary to specify what is considered to be within the estuarine boundaries. Here, we include both the open water of the four major subembayments -- South Bay (SB), Central Bay (CB), San Pablo Bay (SP) and Suisun Bay (SU) -- as well as all other wetlands in tidal contact with this open water. Together, these subembayments will be said to constitute San Francisco Bay (SF). The aquatic boundaries between these subembayments are as specified in the Aquatic Habitat Institute Bay-Delta segmentation scheme (Gunther 1987). The shore boundaries are somewhat harder to delineate due to seasonal and interannual variation in habitat characteristics. Aside from open water, the shore boundaries considered here encompass intertidal mudflats, vegetated tidal marsh, river channels, and rocky shore (see ABAG 1989 for a detailed treatment of wetland habitat classification). An independent assessment was not made for the region south of the Dumbarton Bridge, as certain critical data were not available separately for this area; the relative importance of carbon sources, however, could very well be different from the rest of South Bay.

Morphometric data come from several sources. Data for all open water habitat deeper than mean lower low water (MLLW) were provided by the United States Geological Survey (USGS; J. Burau 1990, pers. comm.). These data, for the nodes of a 0.25-km grid covering the entire Bay, were interpolated from nautical charts (Burau and Cheng 1989). A hypsometric curve, referenced to the MLLW tidal datum, was constructed for each major embayment using these data and the AHI segment boundaries (Fig. A.2, which shows the results only down to 20 m). These curves illustrate, in effect, "typical" cross-sections through the respective embayments. Central Bay clearly stands apart from the others due to its relatively steep slopes. The remaining embayments have quite similar hypsographs, although San Pablo Bay has the highest proportion of shoal area, as evidenced also by its median depth (Table A.1).

Morphometric data for areas above MLLW were taken from other sources. In particular, the areas at mean tidal level (MTL) and mean higher high water (MHHW) were required for our

Table A.1

Morphometry of San Francisco Bay and its four major subembayments referenced to the MLLW tidal datum.

Bay	Area (10^8 m^2)	Volume (10^9 m^3)	Depth		
			Mean (m)	Median (m)	Maximum (m)
SB	4.7	1.9	4.0	2.2	29
CB	2.2	2.5	11	7.7	99
SP	2.6	0.86	3.3	1.5	29
SU	1.0	0.31	3.1	1.8	28
SF	11	5.5	5.3	2.3	99

Note: Based on the the segmentation scheme of Gunther (1987) and the methods of Burau and Cheng (1989).

analysis. First, published values of MTL and MHHW, referenced to the MLLW datum, were averaged for each subembayment (USCOE 1977). Next, the values for MLLW, and thus MTL and MHHW, were referenced to the National Geodetic Vertical Datum (NGVD), again averaged for each subembayment (USCOE 1984). The areas between MLLW and both MTL and MHHW were then determined from tidal stage-area graphs referenced to the NGVD (Morrison 1988). Finally, these incremental areas were added to the data for MLLW as previously determined

Table A.2

Water surface area of San Francisco Bay and its major subembayments at various tidal stages.

Bay	MLLW (10^8 m^2)	MTL (10^8 m^2)	MHHW (10^8 m^2)
SB	4.7	5.5	6.1
CB	2.2	2.4	2.5
SP	2.6	3.2	4.4
SU	1.0	1.2	1.7
SF	11	12	15

Note: Data for MLLW are from Table A.1. The remaining estimates are based on a variety of sources, as described in the text.

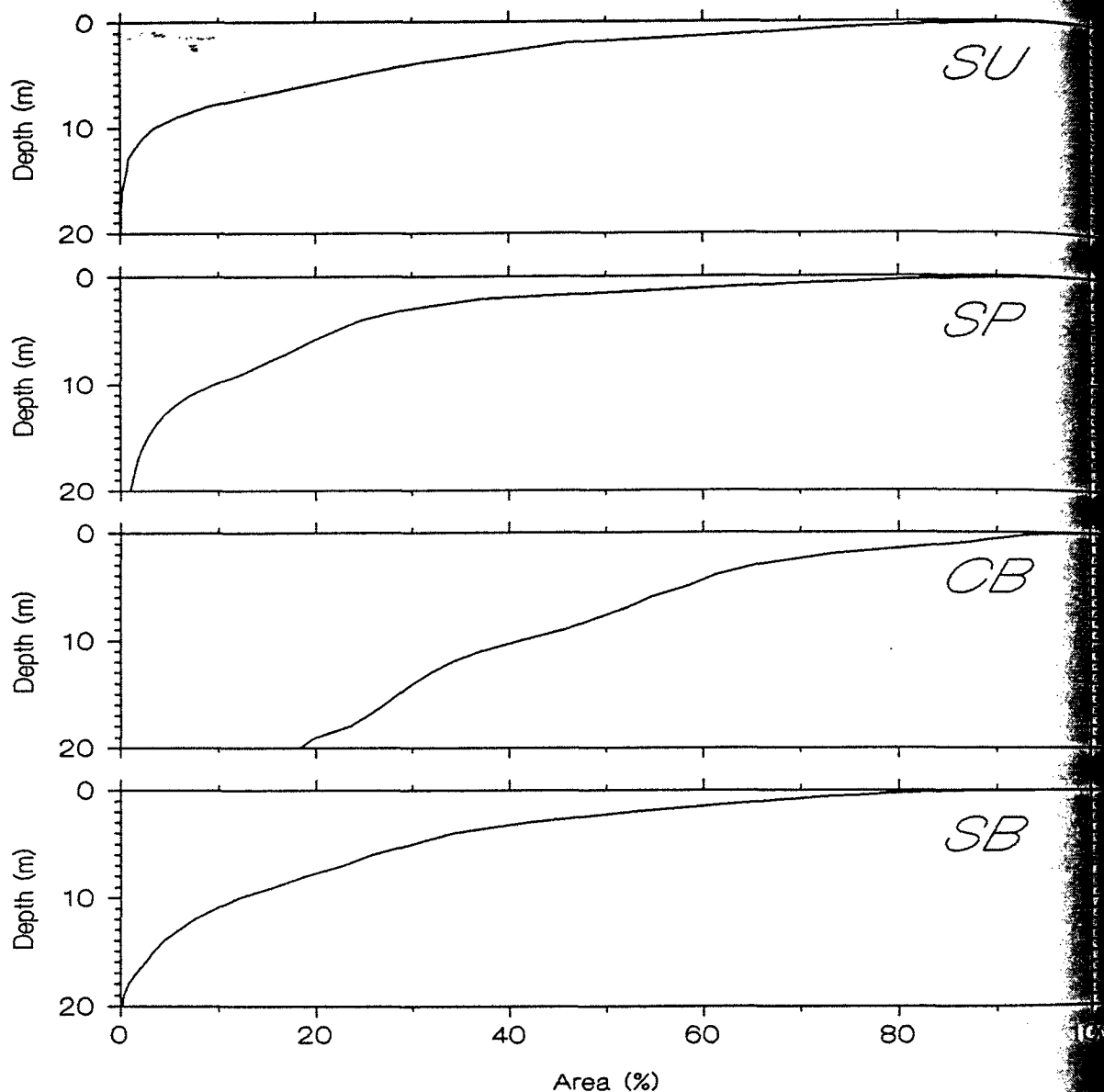


Figure A.2 Hypsographs for the major subembayments of San Francisco Bay (based on the segmentation scheme of Gunther [1987] and the methods of Burau and Cheng [1989]).

from the USGS data (Table A.2; see below for additional information regarding Suisun Bay at MHHW).

Areas for specific habitat types were also required for estimates of certain carbon fluxes. Habitat areas for USGS quadrangle maps were determined from the National Wetlands Inventory (NWI) habitat maps for 1985 and then partitioned among various subembayments (M. Josselyn).

pers. comm.). The partitioning did not correspond exactly with the AHI segmentation scheme; in particular, Central Bay habitat was allocated to either South Bay or San Pablo Bay.

For Suisun Bay, the area corresponding to MHHW was particularly difficult to determine because of the flatness of the hypsograph in the vicinity of MHHW. As this portion of the hypsograph was actually determined with the aid of NWI maps (Morrison 1988), it was decided to use the NWI data for mudflat and tidal marsh directly to define the area between MLLW and MHHW (Table A.2). As far as the carbon flux estimates are concerned, this discrepancy is an issue only for estimates of benthic microalgal production. Furthermore, although habitats do not correspond to any particular tidal datum -- tidal marsh could occur both below MLLW and above MHHW, for example -- the assumption does not affect our conclusions in any way.

A.2 AUTOCHTHONOUS CARBON SOURCES

A.2.1 Phytoplankton

Of the autochthonous organic carbon fluxes to the Bay's food web, phytoplankton productivity has been studied in the most detail (Cloern et al. 1985 summarize and interpret the numerous phytoplankton studies). A particularly valuable data set for the purpose of estimating annual production was collected in 1980, when productivity was determined monthly at six representative stations, including a shoal and channel site in each of South Bay, San Pablo Bay and Suisun Bay (Cloern et al. 1985). Estimates were based on ^{14}C uptake rates in 24-hr incubations under simulated in situ conditions. Respiration rates in the dark were assumed to equal 10% of the maximum (light-saturated) ^{14}C uptake determined from these 24-hr incubations.

The results for these six stations can be converted to estuary-wide estimates of phytoplankton productivity. Because of the estuary's turbidity, positive net primary productivity is confined to a thin layer near the surface where incident light energy is sufficient, the *photic* or *euphotic* zone. The ^{14}C measurements yield an estimate of net productivity within this layer, a quantity known as the *net photic zone productivity* P_{np} ($\text{g C m}^{-2} \text{ d}^{-1}$). P_{np} usually overestimates the organic carbon assimilation in the entire water column because of phytoplankton respiratory losses below the photic zone. A more relevant quantity is the *net water column productivity* P_{nw} , which is simply P_{np} corrected for estimated respiration below the photic zone. The size of the correction depends on the depth of water, so P_{nw} is actually a function of depth even in regions where P_{np} is constant.

The depth Z_p of the photic zone -- usually taken to be the depth by which surface insolation is reduced to 1% -- is a few meters, at most, and varies continuously in both space and time with the changing turbidity. The area over which phytoplankton production takes place also changes significantly with the tide (Table A.2). Because of this complex and dynamic situation, several simplifications and assumptions were necessary to convert the monthly measurements to estuary-wide production estimates (Fig. A.3). First, the water level was assumed to be constant at MTL. Next, each subembayment was divided into a "shallow" and "deep" region at 2 m below MLLW (approximately 3 m below MTL), within each of which net photic zone productivity P_{np} ($\text{g C m}^{-2} \text{ yr}^{-1}$), biomass concentrations b ($\text{mg Chl } a \text{ m}^{-3}$), respiration rates below the photic zone r ($\text{g C m}^{-3} \text{ yr}^{-1}$), and Z_p (m) were assumed to be constant and equal to the annual means determined in 1980. Then, P_{np} was integrated separately over the shallow and deep region, resulting in estimates of net annual photic zone productivity π_{np} (g C yr^{-1}) for each region. Some adjustments were necessary for the margins of each subembayment where photic depth Z_p is greater than the water column depth Z_m . In particular, it can be shown theoretically under certain simplifying assumptions that shoal regions falling entirely within the photic zone have a P_{np} equal to 0.785 of the P_{np} in deeper water where $Z_p < Z_m$. Finally, using the hypsometric data, the volume below the photic zone was determined for both shallow and deep regions. The hypsometric curves were assumed to be linear between

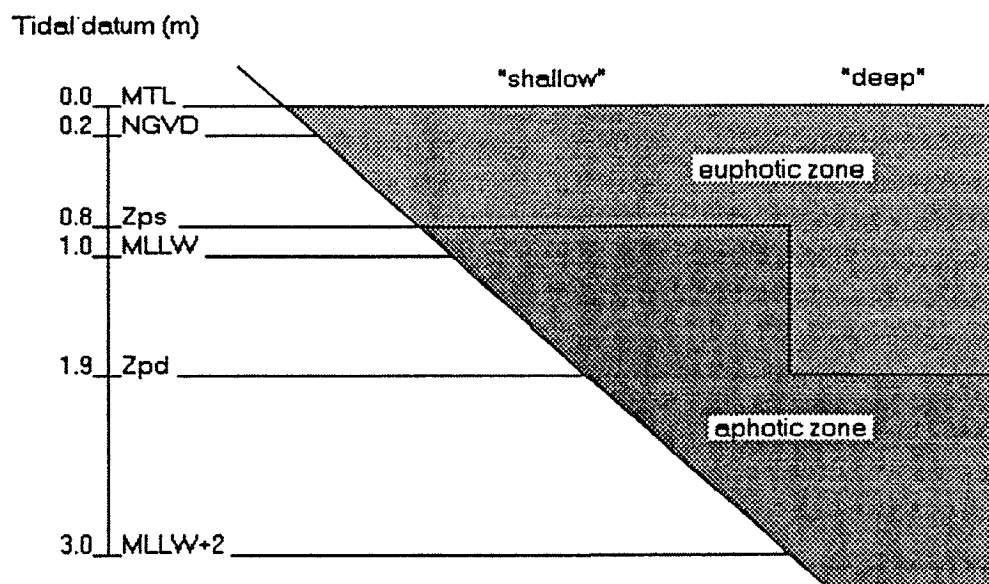


Figure A.3 Schematic cross-section of subembayment illustrating morphometric model used in the estimation of phytoplankton productivity. Values given are for San Pablo Bay.

MLLW and MTL. Respiratory losses were estimated for shallow and deep regions separately and subtracted from the corresponding values for π_{np} , resulting in estimates for net annual water column productivity π_{nw} (g C yr^{-1}).

Central Bay measurements were not reported as part of the intensive 1980 study. Annual values for net photic zone productivity, biomass and photic zone depth are estimated to be $P_{np} = 140 \text{ g C m}^{-2} \text{ yr}^{-1}$, $b = 2.5 \text{ mg Chl } a \text{ m}^{-3}$, and $Z_p = 3.1 \text{ m}$, respectively (Cloern 1987, Fig. 7), without using separate values for shallow and deep regions. A biomass-standardized respiration rate r^b ($\text{g C [mg Chl } a]^{-1} \text{ yr}^{-1}$) of 3 was typical of the 1980 data for the other subembayments (except for an anomalous value for South Bay shoals; Cloern et al. 1985) and was used to arrive at an estimate of $r = 7.5 \text{ g C m}^{-3} \text{ yr}^{-1}$.

Because respiration rates for the aphotic zone of aquatic habitats are so controversial, the data are presented with and without respiration corrections (Table A.3). The data clearly demonstrate how aphotic respiration assumptions have a marked effect on production estimates, accounting for a 30% decrement in net photic zone production for the estuary as a whole and over 50% in the case of Central and Suisun Bays. The differences among subembayments in the importance of aphotic respiration reflects morphometry rather than phytoplankton activity. The

assumption used in Table A.3 -- that r is 10% of light-saturated P_{np} -- may be an overestimate, perhaps even a large one (e.g., Smetacek and Passow 1990).

Respiration, however, is by no means the only source of uncertainty in these estimates. The ^{14}C method itself is characterized by a certain imprecision in the measurement of uptake rates, usually about 10%. Moreover, a number of systematic biases in estimating ^{14}C uptake may be present, including effects due to confinement within bottles, toxic trace metals, "dark bottle" correction, incubation time, and sample fixation (Leftley et al. 1983). An additional underestimate may occur if extracellular products of photosynthesis -- which can sometimes exceed 50% of carbon uptake (Joint and Morris 1982) -- are assimilated and respired by bacteria during the incubation. Further uncertainties are introduced by ignoring the effects of vertical circulation, the existence of vertical and especially horizontal heterogeneity, as well as the presence of tidal marsh vascular plants below MTL that may compete with phytoplankton for insolation. The latter may be a problem especially in Suisun Bay, where California bulrush (*Scirpus californicus*) extends below MTL increasingly from the Carquinez Straits to the Delta (Josselyn 1983). It is not possible to characterize all, or even most, of these uncertainties quantitatively; we can assume, however, that the uncertainty range suggested by respiration alone (Table A.3) should be expanded significantly.

Table A.3

Net annual phytoplankton carbon production for San Francisco Bay and each of its major subembayments.

Bay	π_{nw} (10^9 g yr $^{-1}$)	π_{np} (10^9 g yr $^{-1}$)	$(\pi_{np}-\pi_{nw}) : \pi_{np}$ (%)	Shoal π_{nw} (%)
SB	71	86	18	61
CB	15	30	51	55
SP	39	56	31	76
SU	4.7	11	57	110
SF	130	180	29	66

Note: Net annual water column productivity π_{nw} is calculated by assuming that phytoplankton respiration below the photic zone equals 10% of light-saturated ^{14}C uptake; net photic zone productivity π_{np} assumes that phytoplankton respiration is negligible below the photic zone. Shoal π_{nw} is the percent of π_{nw} occurring in water shallower than 2 m referenced to MLLW. All values are rounded to two digits, but probably only one is significant.

A recent study by Alpine and Cloern (1988) offers some additional information regarding uncertainty. These investigators compared growth rates based on both cell division and ^{14}C uptake at four different sites throughout the Bay, including a simulation of two different mixing conditions for each site. The ratio of the two measures among samples was 1.0 ± 0.8 (95% CL) (Alpine and Cloern 1988, Table 2), implying that there was no systematic error in deducing productivity from ^{14}C uptake but the uncertainty was high for individual samples. An uncertainty range of *at least* $\pm 50\%$ appears to be warranted.

2.2 Tidal marsh vascular plants

Estimates have been made of annual primary productivity for marsh vascular plants at selected sites throughout the Bay (summarized by Josselyn 1983). The values almost all fall within the range of 500 to 1500 g dry wt. $\text{m}^{-2} \text{yr}^{-1}$. No clear difference emerges in the productivity ranges for the dominant salt marsh plants Pacific cordgrass (*Spartina foliosa*) and perennial pickleweed (*Salicornia virginica*); the few higher values were associated with bulrush (*Scirpus californicus* and *S. robustus*) in brackish marsh. Most of the studies estimated annual production either on the basis of a single above-ground end-of-season harvest of live tissue (i.e., maximum live dry weight) or by attempting to account for changes in live and dead tissue over shorter intervals (i.e., the Smalley method).

Both of these methods are known to underestimate production by ignoring losses through decomposition, tidal export and import, leaching from leaves, and herbivory (Hopkinson et al. 1980; Long and Mason 1983). The largest errors are due to ignoring decomposition losses and tidal exchange, with tidal exports usually exceeding imports. Leaching losses are minor compared to shoot production, and grazing losses usually smaller still. The underestimate of production is a serious one, typically by a factor of two or three and sometimes higher. Although the Smalley method is usually more accurate than the maximum live dry weight method, curiously enough a single end-of-season measure of maximum standing crop -- both living and dead dry weight -- often gives the best estimate.

An additional underestimate arises from ignoring below-ground primary productivity (Good et al. 1982). Based on data for smooth cordgrass (*Spartina alterniflora*) on the Atlantic coast, the ratio of below-ground to above-ground annual production appears to average between two and three (Schubauer and Hopkinson 1984). No such comparisons are available for San Francisco estuary tidal marsh plants, but the root-shoot biomass ratio for Pacific cordgrass was estimated to average 3.6 (Mahall and Park 1976), which is typical of smooth cordgrass (Good et al. 1982). There is little reason to believe the ratios of below- to above-ground production will be comparable as well.

Both Atwater et al. (1979) and Josselyn (1983) estimate that emergent vascular plant productivity averages 800 g dry wt. $\text{m}^{-2} \text{yr}^{-1}$ in the San Francisco estuary, reflecting studies that use maximum live dry weight of above-ground biomass or the Smalley method. As little can be said about differences between subembayments at this point, the 15 Bay studies tabulated by

Josselyn (1983, Table 27) must be treated on an equivalent basis; converting to carbon using C:dry wt. ratio of 0.4 (Westlake 1963) yields an average of 420 ± 70 (SE) $\text{g C m}^{-2} \text{ yr}^{-1}$ above-ground productivity for these studies. Based on the previous methodological comments, the actual mean may be quite higher. The discrepancy among the methods is so variable, however, that applying a simple "correction factor" must be considered to be unreliable. As a result, an estimate of above-ground tidal marsh contributions was made by taking these field measurements at face value.

Tidal marsh habitat areas for each subembayment were derived from NWI habitat maps (M. Josselyn, 1990 pers. comm.). Although the habitat area for Central Bay was partitioned between South Bay and San Pablo Bay, the Wetland Habitat Map for San Francisco Bay (B. Chan Meiorin 1990, pers. comm.) suggests that Central Bay tidal marsh habitat is negligible. The partitioning of Central Bay thus has little effect on the values given for South and San Pablo bays. Applying the above-ground productivity estimate to the respective habitat areas results in the following tidal marsh vascular plant productivity values for each of the four subembayments (10^9 g yr^{-1}):

SB	15
CB	0
SP	28
SU	18
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SF	59

Note that the studies tabulated by Josselyn (1983) were conducted during the period 1968-1985 and that the NWI habitat area data were determined for 1985. Assuming that no trend existed in primary productivity on an areal basis, these subembayment estimates thus should be identified with 1985 conditions. As implied in the previous discussion, the stated averages have an uncertainty of $\pm 33\%$ (95% CL) due to differences among sites alone. An additional, perhaps large, systematic underestimate may be symptomatic of the methods used.

Below-ground productivity probably contributes an even greater amount of annual production. In view of the lack of any measurements in the estuary and the large range of values reported in the literature, it is perhaps best to refrain from a quantitative estimate of below-ground production. Because of its confined location, the significance of below-ground production to estuarine energy flow outside of marsh sediment may be smaller than for above-ground production (Schubauer and Hopkinson 1984). But it should be noted that export of below-ground organic carbon can be a significant contributor to the total export, especially in sandy soils. For example, Yelverton and Hackney (1986) estimate an export of $52 \text{ g C m}^{-2} \text{ yr}^{-1}$ due to pore water flux alone from a North Carolina *Spartina* marsh.

The above annual mass contributions of carbon must therefore be considered an underestimate, perhaps even by an order of magnitude. In a later section, tidal marsh is considered from an alternative viewpoint, namely, as an allochthonous source of exported organic carbon for other habitats in the estuary.

2.3 Benthic microalgae

The distinction between those algae that prefer the pelagic ("phytoplankton") and those that prefer the benthic habitat ("benthic microalgae") is often unclear, both because of settling of algal cells from the water column and resuspension of cells from the sediments (Nichols and Matmat 1988). A separation on the basis of preferred habitat, however, need not be of concern here. We need only distinguish between production in the water column and production on the sediments, regardless of what algal types are actually involved in each habitat.

The benthic microalgal community in the estuary has been examined in several studies reviewed by Nichols and Thompson 1985a), most notably in terms of chlorophyll by Thompson et al. (1981) and in terms of species composition by Laws (1983, 1988). J.H. Gregg and A.J. Thorne (pers. comm. 1991) are in the process of analyzing one of the more extensive spatial and temporal surveys of benthic chlorophyll to date (16 stations measured quarterly during water year 1989, and one of these stations sampled 10 times over 18 months). As no measurements of benthic microalgal productivity appear to have been published, however, the only recourse is to estimates based on habitat area and measurements reported in the scientific literature for other systems. Only the crudest of estimates is possible at this stage, both because of the large range of areal production values attributed to other estuaries and the difficulty in defining the relevant habitat areas.

The actual measurement of benthic primary productivity entails unusual technical difficulties, whether measurements are determined through O_2 production, ^{14}C uptake or O_2 gradients. None of the existing measurements in estuaries can be said to be without serious controversy (Admiraal 1984). Furthermore, productivity responds to substrate and a host of environmental factors; although the same can be said for most other natural plant stands, the dynamic nature of the environment is particularly marked in the intertidal zone. Thus, even if the methods were unassailable, the spatial and temporal heterogeneity would still require unusually extensive sampling to adequately characterize annual production (Shaffer and Onuf 1985). The cumulative errors inherent in published estimates imply a great deal of uncertainty.

Several researchers have tabulated results from benthic primary production studies. Knox (1986a) and Colijn and de Jonge (1984), for example, summarize data from over 30 separate sites, including tidal flats and vegetated tidal marsh. As pointed out by the latter authors, most of the annual production values fall within 50 to 200 $g\ C\ m^{-2}\ yr^{-1}$, even though the sites are at widely different latitudes. Most of the exceptions could be explained by extreme conditions (e.g., near estuaries). Other recent studies not tabulated by these authors also fall within the stated range (e.g., Shaffer and Onuf 1985; Varela and Penas 1985; Fielding et al. 1988). We thus adopt this range as the uncertainty range, and the midpoint -- 120 $g\ C\ m^{-2}\ yr^{-1}$ -- as the best estimate, for average benthic primary production for the various subembayments of the San Francisco estuary.

Benthic microalgal production under vascular plant canopies in tidal marshes can be quite high; in the relatively open canopies of some southern California marshes, for example, benthic primary productivity is similar to that of the vascular plant overstory (Zedler 1982; but see discussion in previous section regarding difficulties with vascular plant production estimates). In any case, existing studies do not permit a justifiable distinction between the levels of tidal flat and tidal marsh benthic production. Measurements from both habitat types span the entire range.

It remains to decide on the habitat area -- including both tidal flat and tidal marsh -- suitable for benthic production. If we wish to remain consistent with the simplifications introduced for estimating phytoplankton production, then we must accept as suitable all intertidal areas extending down to a depth of Z_p below MTL. The assumption is that, as for phytoplankton, benthic microalgae lying below the mean 1% surface light level do not receive sufficient insolation for sustained growth. Although benthic chlorophyll *a* may indeed be found on deeper sediments (Thompson et al. 1981), it could very well derive from the settling of planktonic forms. The latter may sometimes dominate not only the benthic microalgal biomass, but also the total biomass of microalgae both on the sediments and in the water column. Settled planktonic algae are an important contribution to the benthic microalgal biomass of Suisun Bay, for example, probably as a result of selective accumulation in the null zone (Cloern et al. 1985). Thus, the presence of chlorophyll in deep sediments is not necessarily evidence for *in situ* growth below Z_p . The upper boundary for the estimate of habitat area is MHHW, by necessity. The hypsometric information extends no further than this tidal datum. Some systematic error may be introduced by the exclusion of high marsh above MHHW -- and perhaps even some tidal flat area -- but most salt marsh above MHHW has disappeared (ABAG 1989).

The entire area from MHHW to a depth of Z_p below MTL was first estimated for each subembayment, using the hypsometric curve for MLLW (Fig. A.2), the areas at MTL and MHHW (Table A.2), and the value of Z_p for each subembayment. As in the calculations of phytoplankton production, linear interpolation was used to extend the hypsometric curves to include MTL and MHHW. The area was not corrected for slope, a relatively insignificant source of error (Fig. A.2). Using an areal production value of $120 \text{ g C m}^{-2} \text{ yr}^{-1}$, the resulting benthic primary productivity estimates for the subembayments are (10^9 g C yr^{-1}):

SB	36
CB	11
SP	19
SU	6.9
<hr/>	
SF	73

Recall that these subembayment estimates have a range of about $\pm 60\%$ due to uncertainty in the mean areal production estimate alone. Additional uncertainties arise from the simplifying assumptions used. The choice of mean photic zone depth is especially critical because of the sensitivity of estimated habitat area to this choice. For example, the value for Central Bay may appear rather high, in view of the steep topography and relatively small intertidal habitat. The

high value is due to its relative clarity and an assumed shoal $Z_p = 3.1$ m (Sec. A.2.1), which could be revised downward if shoal clarity is found to be less than channel clarity.

Further on, we will take the point of view that tidal marsh productivity, including the benthic microalgal component, is an allochthonous contribution to the open water-intertidal mudflat system. In that case, the contribution from tidal marsh benthic microalgae would be accounted for in the total tidal marsh export. The residual amounts contributed only by subtidal areas and intertidal mudflats can be estimated if we first subtract the amounts attributable to tidal marsh habitat using NWI map data for 1985. Once again, we assume that the small amount of Central Bay tidal marsh habitat can be ignored. The resulting benthic productivity values for open water and intertidal mud flats are (10^9 g C yr^{-1}):

SB	32
CB	11
SP	12
SU	1.7
<hr/>	
SF	57

Together with the original estimates that included tidal marsh habitat, these estimates demonstrate that a substantial part of total benthic microalgal production may take place on tidal marsh sediments.

Note that these estimates are based on photic zone depths in 1980, with a correction for tidal marsh area from the 1985 NWI data. In the case of South Bay, net tidal marsh area changed little since 1958 -- the most recent NWI analysis prior to 1985 (ABAG 1989) -- and the South Bay estimate thus can be considered valid for 1980. The Central Bay estimate is also applicable to 1980, as Central Bay needed no correction for tidal marsh area. The 1958 NWI data has not been digitized for San Pablo or Suisun bays, however, so we must assume that marsh areas were essentially the same in 1980 and 1985 in order to apply the above estimates to 1980.

A.2.4 Seagrasses

Eelgrass (*Zostera marina*) is usually the dominant seagrass species in temperate estuaries of both the Atlantic and Pacific coasts of the U.S. and, indeed, appears to be the only seagrass of significance in the San Francisco estuary (Wyllie Echeverria and Rutten 1989). Its actual distribution in the Bay is limited, however, covering a total of only 128 ha, on the basis of a 1987 survey. Most of the eelgrass is found in Central Bay, which has 17 separate stands totalling 83 ha. San Pablo Bay has a single stand of 50 ha directly north of Point San Pablo and South Bay has a few stands totalling 25 ha in the vicinity of Alameda. An additional patch less than 1 ha in area is located at Coyote Point near San Mateo.

No productivity measurements have been made for these eelgrass stands. Values reported in the literature cover a wide range, from as little as 58 to as much as 1500 g C m⁻² yr⁻¹ (Ma 1972), including significant contributions from below-ground rhizome growth (Rasmussen 1977) and epiphytes (Penhale 1977). Most temperate eelgrass communities have productivities between approximately 100 and 500 g C m⁻² yr⁻¹, including those of the subtidal Pacific Coast (Phill 1974). Using a mean value of 300 g C m⁻² yr⁻¹, the estimated values of seagrass productivity for the major subembayments are as follows (10⁹ g C yr⁻¹):

SB	0.075
CB	0.16
SP	0.15
SU	none
<hr/>	
SF	0.38

As implied in the above discussion, these estimated productivities have a range of $\pm 70\%$ to uncertainty in the mean productivity value alone. Also, as the San Francisco estuary stands consist mostly of clumps rather than dense meadows, the actual productivity values may be the lower part of the reported range for temperate eelgrass communities.

During typical winters, the northernmost stand in San Pablo Bay is subjected to salinity as low as 6 ‰ (Conomos et al. 1985), which may represent the low end of the salinity range for *Zostera* (Rasmussen 1973). This could be construed as evidence that low salinity prevents penetration further northward in the estuary. On the other hand, light availability is usually a critical factor determining seagrass distribution in turbid environments (e.g., Wetzel and Penhale 1983), and winter turbidity is often at a maximum north of the eelgrass beds (Conomos et al. 1985). The interpretation is further complicated by the relative absence of beds in the upper South Bay, where -- based on the location of beds elsewhere in the estuary -- the waters are clearly within the salinity and turbidity range of eelgrass. Substrate, pollutants or the vagaries of colonization and extinction could conceivably have a role. Unfortunately, the absence of historical data on seagrass communities precludes a search for environmental correlates of distributional change. Further, the information on current beds includes only the horizontal spatial boundaries. An unequivocal explanation of eelgrass distribution is thus not possible at this time.

A.2.5 Macroalgae

Most macroalgae in the estuary are restricted to Central Bay (Silva 1979; Josselyn West 1985), although colonies do extend down into the southern part of South Bay and through the Carquinez Straits into Suisun Bay. Changes in percent cover of macroalgae have been followed on a seasonal and interannual basis at several sites, but no attempt has been made to assess the total standing crop in any of the major subembayments. The presence of numerous individual colonies of varying dimensions and depth render this task virtually impossible.

patchy nature of macroalgal distribution reflects both the availability of suitable substrate -- particularly solid substrate such as rocks, pilings, and shells -- and the mobility of drift communities floating along the estuary bottom. This same substrate dependence, however, limits total macroalgae coverage on an estuary-wide basis. Thus, despite the fact that macroalgae have a capacity for high productivity in the estuary (Shellem and Josselyn 1982), their contribution to annual primary production is probably not significant (M. Josselyn 1990, pers. comm.). Actual contributions to individual subembayments are unknown, however.

Although macroalgae are of little importance to the estuary-wide carbon budget, they can form nuisance blooms of local significance. In South Bay, drift macroalgae can form unsightly, noxious accumulations along Alameda (Horne and Nonomura 1976). Decaying *Polysiphonia* blooms can smother benthic communities and alter the local benthic environment (Nichols 1979). In Central Bay, the green macroalgae *Ulva* and *Enteromorpha* attained dense accumulations off Albany in past summers (Bain et al. 1968); a nearby sewage treatment plant and the configuration of the basin were implicated. In San Pablo Bay, a bloom of *Cladophora* clogged cooling water intake pipes in 1979 (California Legislature 1979). These macroalgal blooms can disrupt recreational (beaches), industrial (cooling water) and food web (benthos) activities, and the possibility of increased bloom frequency in the future cannot be dismissed. Accordingly, the factors responsible for their occurrence should be of some concern. In San Pablo Bay, the blooms have been attributed to the coincidence of optimal light, temperature, salinity and tidal conditions (Josselyn and West 1985), but current understanding is insufficient to make reliable forecasts.

A2.6 Other Autochthonous Sources

Photosynthetic bacteria inhabit areas where both light and reduced sulfur in the form of H_2S are available, usually on anoxic sediments where S^{2-} has been produced through dissimilatory reduction. In these circumstances, H_2S is used as an electron acceptor in photosynthesis, in contrast to the use of H_2O by conventional plants growing under aerobic conditions. The photosynthetic production is a true contribution to the organic carbon budget, although any energy subsidy arising from the use of locally-produced H_2S should be discounted. In any case, the habitat available to photosynthetic bacteria is a subset of the area for benthic macroalgal production. As the latter was estimated on the basis of mean productivity and habitat area, the contribution of photosynthetic bacteria was included implicitly. It is possible that the productivity values used are not characteristic of photosynthetic bacteria in the Bay, but at least visual observation indicates that they occupy little area outside of the salt-evaporation ponds, which are essentially isolated from Bay waters (Nichols and Pamatmat 1988).

Epiphytic algae, mainly diatoms, are potentially large contributors to estuarine production, about 10% of total primary production for some estuaries (Penhale and Smith 1977). They attach to submerged parts of vascular plants, macroalgae and seagrasses. Epiphytic production does not, however, alter the above estimated autochthonous contributions to the organic carbon budget of the Bay. In the case of tidal marsh vascular plants, for example, any contribution by

epiphytic growth was accounted for implicitly by the method used, namely, harvest of total biomass. Conclusions about macroalgal production will not be changed by including consideration of epiphytic growth: The lack of macroalgal significance is based on inadequate habitat area, not on low productivity. Finally, the range of seagrass productivities was also based on measures (^{14}C uptake, O_2 production, biomass changes) that implicitly included epiphyte production. In any case, epiphytic production is usually at the expense of the host plant, due to competition for light or nutrients (e.g., Phillips et al. 1978); epiphytes thus may result in a partition of production rather than a change in the total.

A.3 ALLOCHTHONOUS CARBON SOURCES

A.3.1 Delta outflow

The potential significance of Sacramento and San Joaquin River loading of organic carbon can be appreciated by noting that Delta outflow has recently ranged from 3.1 (1976-77) to 79 (1982-83) km³ yr⁻¹, while the entire Bay has a MLLW volume of only 5.5 km³. Schemel (1984) has compiled the only data set that bears directly on this question. Based on biweekly flow-weighted measurements of DOC at Rio Vista during 1980, Schemel (1984) estimated the Sacramento River flow of DOC to be 150×10^9 g yr⁻¹, with a mean annual flow-weighted DOC concentration of 5.0 mg l⁻¹.

POC data were collected only from April through December, so an estimate of annual POC transport requires additional assumptions. As there was no apparent seasonal trend in the ratio POC:DOC, based on the 9 months of overlapping data, the mean of this ratio -- 0.10 ± 0.02 (SE) -- was used to estimate an annual POC load of 15×10^9 g yr⁻¹. The corresponding annual mean flow-weighted POC concentration was 0.50 mg l⁻¹. The POC:DOC ratio could be seriously biased by the absence of January-March data, as 65% of annual river discharge took place during this period. Schemel (1984) pointed out that, even for the April-December period, actual POC:DOC ratios were probably higher, as samples were taken from near the surface and the ratio probably increased with depth. Peterson (1979), for example, estimated a POC load of 9×10^9 g yr⁻¹, using a POC:sediment ratio of 3%. Even if a ratio of 1% is used -- more typical of surface sediments deposited within the Bay (Thomson-Becker and Luoma 1985) -- the resulting POC load is twice the amount estimated from Schemel's (1984) surface samples.

Based on data for chlorophyll and its degradation products, much of this POC appears to be river-borne phytoplankton and phytoplankton-derived detritus. Chlorophyll measurements of near-surface samples at Rio Vista were aggregated by month (and interpolated for the few months where no chlorophyll measurements were collected). The data were combined with river flow measurements and an assumed C:Chl *a* ratio of 50 to arrive at a POC flux of 6×10^9 g C yr⁻¹ associated with chlorophyll *a*. Pheopigments averaged 50% of chlorophyll *a* at Rio Vista during 1980 (Ball 1987a, Fig. 3b), suggesting a POC flux totalling 9×10^9 g C yr⁻¹ for both phytoplankton and phytoplankton-derived detritus, or about 60% of the measured POC flux. Becker and Schemel (1979) found that the stable isotope composition of POC just upstream of Suisun Bay was characteristic of riverine phytoplankton, not of land plants, a result that is consistent with the estimates presented here. Also, as pointed out by Ball (1987a), phytoplankton blooms in the western Delta are often carried into Suisun Bay when flows exceed 300 m³ s⁻¹.

Because the Sacramento River contributed 76% of Delta inflow and an even larger fraction of Delta outflow, the composition of the Delta outflow was probably similar to the composition of the river (Schemel 1984). In the absence of adequate organic carbon measurements for the San Joaquin and east side rivers, the annual load of TOC into Suisun Bay can be estimated by multiplying Sacramento River transport by the ratio of Delta outflow to Sacramento River flow,

a factor of 1.08 in 1980. Summing the estimates for DOC and POC, the 1980 TOC load in Suisun Bay was about $180 \times 10^9 \text{ g yr}^{-1}$, based on the data set of Schemel (1984). Recalling the more representative sampling of the vertical POC distribution could result in an upward revision of this estimate, $150\text{-}250 \times 10^9 \text{ g yr}^{-1}$ may be taken as the range of uncertainty.

All allochthonous sources, such as riverine loading, are capable in principle of supplying substrate for chemoautotrophy. Chemoautotrophic bacteria obtain their carbon from CO_2 but their energy from reduced inorganic substances, including nitrogen and sulfur species, Fe^{+2} and H_2 . *Nitrosomonas* and *Nitrobacter*, for example, oxidize NH_3 and NO_2^- , respectively, in the process known as nitrification. The carbon incorporation represents a true addition to the organic carbon pool of the estuary, as long as the substrate originates outside the estuary. In the case of Delta discharge, the only river-borne substrate of any magnitude appears to be NH_3 . Direct measurements of nitrification cannot assess the importance of allochthonous contributions, but nitrification assays include substrate produced by ammonification of organic matter within the estuary. External loading, however, establishes an upper limit of nitrification contributions to the food web. Approximately $2 \times 10^9 \text{ g yr}^{-1}$ $\text{NH}_3\text{-N}$ is contributed by Delta outflow (estimated from the data of D.H. Peterson et al. 1985). On the other hand, 35 mol of NH_3 are required for each mol of CO_2 fixed (Atlas and Bartha 1987). The entire riverine NH_3 load can thus support a maximum of only $0.05 \times 10^9 \text{ g C yr}^{-1}$ chemoautotrophic production. The actual amount utilized in nitrification is undoubtedly much lower, considering the possibility of outwelling (i.e., release through the Golden Gate) and chemical oxidation. Uptake by phytoplankton is also a likely fate for much of this NH_3 loading (Peterson 1979), but this could actually be considered an energy subsidy in the sense that it offsets energy requirements for reduction of NO_3^- , which would otherwise need to be assimilated.

The consequences for the food web of riverine organic carbon may be far less than implied by the high loading values. River-borne organic carbon arises from several sources, including phytoplankton, aquatic macrophytes, litter from terrestrial vegetation, leaching of soils, sewage effluent, and so on. The lability of this detritus -- that is, the ease with which it can be utilized -- is highly variable and is often characteristic of the source. Municipal sewage effluent degrades relatively quickly, for example, while humic substances formed in the breakdown of terrestrial plant material are relatively long-lived (Wetzel 1975 provides a detailed discussion of detritus and decomposition).

Refractory humic substances often constitute more than 90% of the DOC in river water (Reuter 1977), suggesting that a large fraction of this DOC may pass through the estuary unchanged, not participating in the estuarine carbon cycle. Although the breakdown time for humic-rich riverine DOC may be much shorter than previously thought (Keiber et al. 1990), it is still too long for these substances to be a source of organic carbon to the estuarine food web.

In the case of POC, refractory materials may be avoided by consumers or, even if ingested, may contribute little to energy needs. As with refractory DOC, microbial transformation may be required before refractory POC can enter the food web. On a global basis, typically about 35% of riverine POC consists of highly labile materials such as sugars

amino acids (Ittekkot 1988). Depending on the hydraulic residence time within the estuary, less labile material also may become available. The exact amount depends both on the nature of the river-borne material and the hydraulic residence time in the estuary.

Bacterial processes may play an essential intermediary role between allochthonous sources of organic matter and larger planktonic or benthic invertebrates. Riverine phytoplankton, for example, must undergo osmotic stress within the vicinity of the entrapment zone, probably liberating organic material for bacterial processing. Also, detrital material from upstream may be colonized by bacteria and rendered more desirable and nutritious for consumers such as *Neomysis mercedis*, which often has abundant detritus in the gut (Kost and Knight 1975).

No studies appear to have been conducted explicitly on the suitability of organic carbon from Delta discharge as a food for primary consumers, but some pertinent indirect evidence exists. Five-day Biochemical Oxygen Demand (BOD₅) was measured at several Department of Water Resources (DWR) stations along the Sacramento River between Rio Vista and Chipps Island from 1968 to 1977. The sites (and periods of record) were as follows: below the Rio Vista Bridge (D24, 1968-1970); at Emmaton (D22, 1968-1970); above Point Sacramento (D4, 1973-1977); and at Chipps Island (D10, 1968-1970, 1973-1977). Data were collected approximately monthly during the indicated periods. No differences in the mean values could be found among sites for the periods 1968-1970 (D24, D22, D10) or 1973-1977 (D4, D10). No trend in the annual mean could be detected at Chipps Island, the only station for which a long record existed. The mean BOD₅ value was 1.3 ± 0.1 (SE) mg l⁻¹. If we assume a C:O₂ molar ratio of 1, this level of BOD₅ corresponds to 0.49 mg l⁻¹ organic carbon, which can be considered an indication of "readily available" organic carbon. The lack of any long-term trend suggests that we might apply this mean to 1980 as well. Recall that measured TOC averaged 5.5 mg l⁻¹ at Rio Vista in 1980, implying that, of the total 180×10^9 g yr⁻¹, at least 16×10^9 g C yr⁻¹ -- approximately 10% -- was readily available for assimilation and metabolism by bacteria and perhaps higher organisms. This value is consistent with the results from global studies quoted above.

It is useful to examine the magnitude of BOD₅ loading from Central Valley point source dischargers. A minimum estimate for the early 1970s -- when secondary treatment was beginning to expand -- as well as for 1979, has been assembled by Hansen (1982). The 1979 values amount to 3.2×10^9 g BOD₅ yr⁻¹, equivalent to a TOC of 1.2×10^9 g C yr⁻¹, or 1.6×10^9 g C yr⁻¹ if we use convert the BOD₅ to ultimate BOD using typical values for sewage (Sec. 3.3). The actual values may be higher than this minimum estimate. On the other hand, much of this material may already be oxidized before it reaches the Bay. In any case, there is no evidence that point source discharge upstream of Suisun Bay is a major component of TOC loading from Delta outflow.

A.3.2 Tidal marsh export

An alternative way to assess the influence of marsh productivity is to examine only organic carbon export. Whatever the production level, some will be utilized by consumers within the tidal marsh habitat itself and some will be exported to other habitats in contact with the marsh through water transport. The magnitude of this export is of some interest, as many consumer organisms are excluded from tidal marsh by their environmental needs. For the organisms, it is preferable to consider tidal marsh production as an allochthonous contribution of organic matter. No relevant measurements of organic carbon flux between tidal marsh and other habitats of the Bay have been published, although some studies exist on nitrogen exchange (Bucholz 1982). In the absence of any direct measurements, we must turn to results from other estuaries.

Nixon (1980) characterizes the magnitude of TOC flux from tidal marsh as lying in a range of $100-200 \text{ g C m}^{-2} \text{ yr}^{-1}$, based on data from 5 studies. Four of the marshes actually have values lying within an unusually small range of $100-165 \text{ g C m}^{-2} \text{ yr}^{-1}$; the remaining marsh is a net importer of TOC, but this appeared to be attributable to intense filter feeding of a mussel bed near the mouth of the tidal inlet. The agreement among the sites is quite remarkable, in view of the uncertainties in measuring water exchange (Nixon 1980) and other possible errors due to the highly intermittent nature of major transport events and an unmeasured but possibly significant bedload transport (e.g., Odum et al. 1979). The number of cases is small, however, and the agreement may be fortuitous. For example, indirect estimates of TOC export were about $400 \text{ g C m}^{-2} \text{ yr}^{-1}$ for two studies of Barataria Bay, Louisiana (Day et al. 1973; Kirby and Gosselink 1976), as well as for Sapelo Island, Georgia (Teal 1962). Exports of more than $400 \text{ g C m}^{-2} \text{ yr}^{-1}$ were estimated for the North Inlet in South Carolina (Kjerfve and McKellar 1979; Chrzanowski et al. 1983). Modeling studies based on data for *Spartina anglica* stands in the Severn Estuary also suggest exports of more than $400 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Randerson 1986). In contrast, Borey et al. (1983) estimated an export flux of only $20-30 \text{ g C m}^{-2} \text{ yr}^{-1}$ for Galveston Creek, Texas. Roman and Daiber (1989) recently estimated a flux of $110 \text{ g C m}^{-2} \text{ yr}^{-1}$ for Canary Creek, Delaware -- more consistent with a range of $100-200$ -- but transport by coastal storms was not included. To summarize, the uncertainty range for TOC export fluxes extends from negative values up to about three times the "typical" estimate of $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ implied by Nixon (1980).

The estimates are further complicated by the important role of reduced sulfur compounds in marsh metabolism. Anaerobic decomposition in which SO_4^{2-} is the major electron acceptor is the dominant decomposition pathway in at least some saltwater marshes. The energy released during anaerobic respiration is only about 25% of that for aerobic respiration; the remainder is stored in reduced sulfur compounds such as H_2S , which may be subsequently utilized as an energy source by various chemoautotrophic organisms in the marsh or adjoining habitat. In the Great Sippewissett marsh, about 75% of the annual energy export was actually in the form of reduced sulfur compounds (Howarth and Teal 1980; Peterson et al. 1983). Although sulfur reducers are definitely active in the San Francisco estuary (Oremland and Silverman 1982; Oremland et al. 1982), the allochthonous contribution of reduced sulfur compounds from

marshes remains unknown. Export of reduced sulfur would, however, increase the allochthonous energy contributions of tidal marsh beyond that estimated on the basis of organic carbon export alone. At the Great Sippewissett, for example, if transformed into organic carbon with 25% efficiency, reduced sulfur export is equivalent to almost $200 \text{ g C m}^{-2} \text{ yr}^{-1}$.

As in the case of river-borne organic carbon, the issue of *availability* arises for tidal marsh export. The availability of exported material is a complex and controversial subject (reviewed by Valiela 1984; Mitsch and Gosselink 1986; and especially Mann 1988), and the quantitative significance of this issue for the San Francisco estuary is unknown.

Bearing these caveats in mind, a mean export value of $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ results in the following annual mass exports for the tidal marshes of each subembayment, based on the NWI habitat maps for 1985 (10^9 g C yr^{-1}):

SB	5.2
CB	0
SP	9.8
SU	6.4

21

As discussed in the context of benthic microalgal productivity (Sec. A.2.3), the South and Central bay estimates can be applied to 1980 as well. For the other two subembayments, it is necessary to assume that tidal marsh areas changed little between 1980 and 1985.

A3.3 Point sources

The term "point source" usually refers to a source of material load to the estuary that filters at a discrete location and can be identified as the waste stream of an individual discharger. An example is the discharge from a municipal wastewater treatment plant. Point source dischargers in the Bay area are regulated by the California Regional Water Quality Control Board, San Francisco Bay Region (CRWQCB-SFBR), which compiles the monitoring data of individual dischargers. Gunther et al. (1987) describe the state of this data set in some detail. At the end of 1986, 205 permits were in effect for point-source discharges to San Francisco Bay, although not all were active.

Organic carbon data (i.e., TOC, DOC, and POC) are not part of the required monitoring program for point sources. As a result, we are compelled to make inferences about carbon loading from the routine measurements of Biochemical Oxygen Demand (BOD). BOD values correspond to the metabolizable fraction of the organic carbon load, and thus may be more germane than TOC to the issue of energy supply to the food web. In order to compare with the contributions from other sources, however, it is necessary to attempt some kind of conversion to our common currency, namely, organic carbon. Although interchangeability of TOC and BOD

is often assumed in mathematical models of biological oxidation, experimental and field studies suggest that the TOC:BOD ratio is highly variable (e.g., Kim 1987; Pinter et al. 1980). The lack of correspondence is not surprising, considering the variety of carbon sources entering the waste stream, particularly when industrial effluent or urban runoff are combined with domestic waste. The theoretical TOC:BOD ratio depends not only on the material undergoing decomposition, but also on the degree of treatment; the ratio of refractory to labile organic materials increases in treatment, resulting in a progressive increase in the TOC:BOD ratio (Tittizer 1978).

Although it is difficult to specify a priori a range for TOC:BOD, we can arrive at a rough limit on theoretical grounds. Let us assume that the sewage has a respiratory coefficient -- that is, C:O₂ molar ratio -- of 1, which is typical of carbohydrates and even proteins before nitrification of NH₃. This may be appropriate for San Francisco Bay, in which about 90% of the BOD loading is due to municipal and only 10% to industrial sources (T. Wu 1990, pers. comm.). A respiratory coefficient of 1 implies a TOC:BOD mass ratio of 0.38. Dischargers usually report BOD₅, which is typically two-thirds of the ultimate BOD in domestic sewage (Warren 1971). The TOC:BOD₅ ratio is thus 0.57. This value would be reduced if some of the ammonia released were oxidized as well. In the case of phytoplankton, for example, where C:N molar ratio is typically 16, the complete nitrification of NH₃ to NO₃⁻ would result in a TOC:BOD₅ of 0.43. As nitrification facilities, however, are not integrated into some of the larger treatment plants in the Bay area -- for example, the East Bay Municipal Utility District (EBMUD) plant -- most sewage nitrogen reaches the Bay as NH₃ (Conomos et al. 1979, T. Wu 1990, pers. comm.) and an intermediate TOC:BOD ratio is probably appropriate for proteinaceous materials. Moreover, although many of the fatty substances in municipal sewage are removed during primary treatment, a colloidal suspension of fats may survive even secondary treatment as observed at the EBMUD plant (W. Hellier 1990, pers. comm.); these fats would also tend to decrease the TOC:BOD ratio. Accordingly, we choose here a mass ratio of 0.5, somewhat less than the value corresponding to a respiratory coefficient of unity; the amount of metabolically available TOC is thus assumed to be at least half the mass of the BOD load. In fact, a range of 0.5 to 1 is commonly encountered for municipal raw sewage and primary effluent (e.g., M. J. 1970; Iskandar 1978), where one would expect the lowest values. A ratio of 0.5 thus seems to be a reasonable minimum for municipal waste, based on both theoretical and empirical evidence. The high end of the range, however, is uncertain.

The CRWQCB-SFBR has compiled municipal BOD₅ loadings to San Francisco Bay during the period 1955-1985, by subembayment (CRWQCB-SFBR 1987). The estimated minimum TOC loadings in 1980, assuming a TOC:BOD₅ of 0.5, are (10⁹ g C yr⁻¹):

SB	6.6
CB	4.7
SP	0.18
SU	1.5
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SF	13

Industrial discharge, not included in the above loading estimates, accounted for an additional 5% BOD₅ load, at least in 1985 (T. Wu, pers. comm. 1990).

Although EBMUD discharges into a region considered part of Central Bay according to the AHI segmentation scheme, the CRWQCB-SFBR classifies EBMUD as a South Bay discharger. EBMUD had an average flow of $120 \times 10^9 \text{ l yr}^{-1}$ during the period 1984-1986 (Günther et al. 1987), which is about 20% of the total South Bay point source discharge for 1985 (CRWQCB-SFBR). Thus, the South Bay value should be decreased somewhat and the Central Bay value increased by the same amount. As will become clear, however, omission of this adjustment does not affect any conclusions.

It is also of interest to calculate the implied TOC concentrations in waste discharge given the estimated "available" TOC loads and the waste flow for each subembayment. Estimates were made for 1985 -- year of the most recent CRWQCB-SFBR compilation -- in order to compare with recent actual TOC measurements. These implied TOC concentrations are (mg l^{-1}):

EB	4.8
SA	12
SP	9.3
ST	10
<hr/>	
SW	6.1

Some data are available for effluent TOC concentrations from the San Jose/Santa Clara Water Pollution Control Plant, which is the single largest discharger in the South Bay. In autumn of 1989, samples for TOC analysis were collected from Artesian Slough, which receives discharge from the plant (T. Grovhoug 1990, pers. comm.). The low salinities of these samples indicated that they were, indeed, mostly sewage effluent, largely undiluted with Bay water. The samples contained 7.4-8.4 mg l^{-1} TOC. Certain effluents have much higher TOC concentrations. For example, based on daily TOC measurements from 12 June 1989 through 1 June 1990 (W. Jellier 1990, pers. comm.), the mean effluent TOC for EBMUD is 30 mg l^{-1} . Although these data are consistent with the estimates of 4.8 and 9.3 mg l^{-1} , respectively, for "available" TOC, they do raise the possibility of much higher values. A meaningful uncertainty range cannot be given, however.

As in the case of river-borne NH_3 , sewage NH_3 must be considered a potential fuel for chemoautotrophic contributions to the organic carbon pool. The maximum rates of nitrification in estuaries have been measured, in fact, directly beneath sewage outfalls, where high NH_3 and sufficient O_2 occur (Billen 1975; Vincent and Downes 1981). Point source waste loads of $\text{NH}_3\text{-N}$ can be estimated by combining $\text{NH}_3\text{:BOD}$ ratios for 1975 waste loads in each subembayment (Peterson 1979) with the 1980 BOD data (CRWQCB-SFBR 1987). The resulting loads total $3.3 \times 10^9 \text{ g yr}^{-1} \text{ NH}_3\text{-N}$, similar to the river-borne load and equally unimportant.

A.3.4 Runoff

The category of runoff is defined to be all loads to the Bay carried by inflowing water are not included in Delta outflow, tidal marsh export, or point sources. This category is equivalent to the load contributed by local rivers and creeks, as they may also carry sewage (e.g., Coyote Ck.) and tidal marsh contributions (e.g., Petaluma R.). In fact, summer inflow in the South Bay may be largely due to treated wastewater effluent. The loading from runoff must therefore be assessed through indirect methods.

Russell et al. (1982) tabulated BOD₅ loading from several sources, including surface runoff, for 1978. For the entire Bay, the runoff BOD₅ was 6.7×10^9 g yr⁻¹, which, according to our previous discussion on point sources, may be equivalent to at least 3.4×10^9 g C yr⁻¹. The amounts were not partitioned among the various subembayments and the basis for estimates was not explicitly detailed.

An alternative estimate can be made by examining typical TOC concentrations in runoff water. Silverman et al. (1985) measured TOC at 15 runoff stations over a 12-month period (1984-1985). The mean value was 8.1 ± 0.9 (SE) mg l⁻¹; variability due to storms and land use was small. A more recent study of nonpoint sources in the San Pablo Reservoir watershed similarly found a TOC concentration of 8-10 mg l⁻¹, regardless of whether the land use was residential, commercial or open space (Smith 1989). Runoff volumes for 1977, 1981, and 1982 were assessed by Gunther et al. (1987). Estimates were based on precipitation data from the National Climatic Data Center (NCDC) and runoff coefficients developed by the National Oceanographic and Atmospheric Administration (NOAA) for different land use types. The runoff estimates treat Central and San Pablo bays as a unit, and we are consequently forced to do the same here for organic carbon loading. If we assume that 8 mg l⁻¹ is a characteristic TOC concentration in runoff and use runoff volumes for 1981, then the corresponding loading is (10^9 g C yr⁻¹):

SB	3.1	(0.96-4.8)
CB	-	
SP	1.8	(0.80-2.4)
SU	0.64	(0.29-0.80)
<hr/>		
SF	5.5	(2.0-8.0)

The values in parentheses represent the range based on estimated runoff volumes for a dry year (1977) and a wet year (1982). The range is clearly consistent with the values based on tabulation by Russell et al. (1982). Although runoff volumes were not estimated for 1980, it was a precipitation year intermediate between 1981 and 1982. The loading from runoff probably also intermediate between the values for 1981 and 1982. The loading values for 1980 are therefore estimated as 4×10^9 g C yr⁻¹ for South Bay, 2×10^9 for Central plus San Pablo Bay, and 0.7×10^9 for Suisun Bay.

5 Other allochthonous sources

A variety of other possible allochthonous sources can be entertained. Russell et al. (1982), for example, estimated an aerial fallout of 1.8×10^9 g BOD₅ yr⁻¹ to the surface of the Bay in 1978, implying atmospheric deposition of at least 0.90×10^9 g TOC yr⁻¹. On the basis of data from Chesapeake Bay, Gunther et al. (1987) extrapolated a total hydrocarbon deposition of only 0.45×10^9 g yr⁻¹ to San Francisco Bay.

Oil spills are also common in the Bay, although the mass loading from spills was estimated to be only about 0.073×10^9 g yr⁻¹ of petroleum hydrocarbons in 1986 (Gunther et al. 1987) and presumably even less in terms of TOC. A large interannual variability in spills would not be surprising, but annual spillage during the period 1984-1986 was quite consistent at $0.09 \pm 0.01 \times 10^9$ g yr⁻¹ petroleum hydrocarbons.

Groundwater loading appears to be a completely unknown source. Russell et al. (1982) did not include groundwater among the significant freshwater sources to San Francisco Bay (but there was no explicit justification). If groundwater flow is indeed minor compared to, for example, runoff, then organic carbon loading from groundwater is probably negligible as well; there is no reason to expect much higher concentrations of organic carbon in groundwater than in runoff.

A.4 EXCHANGE PROCESSES

A.4.1 Circulation and mixing

Exchange processes include forms of transport that can transfer organic carbon both and out of the region of interest, that is, San Francisco Bay or its major subembayments. could break down the net flux into the sum of a source and a sink and thus avoid the creation of this intermediate category of processes. But when the source and sink are so closely linked -- especially in the case of turbulent mixing across boundaries -- both efficiency and understanding are better served by considering the two fluxes together.

Physical exchange processes have a great potential for modifying the carbon budget at the junction between adjoining subembayments, as well as at the Golden Gate, where water moves both seaward and landward due to a number of different forces, including tides, Delta discharge, density gradients, and the wind. As Delta discharge greatly exceeds Bay evaporation on an annual basis, the net yearly flux of water is, of course, in a seaward direction, but there is no *a priori* reason to conclude the same for DOC and POC. In the Grevelingen estuary, for example, import from the North Sea accounts for at least half of the POC sources (Wolff 1979). The actual net fluxes depend not only on the direction and intensity of advective and diffusive transport, but also on the distribution of organic carbon in the plane of the interface between estuary and ocean.

Conomos (1979), Walters et al. (1985), and Smith (1987) have reviewed mixing and circulation processes in the estuary. The understanding of hydrodynamic behavior in the Bay is considerable. Nonetheless, the magnitude of organic carbon exchange cannot be estimated to any useful degree of certainty, either between subembayments or through the Golden Gate. Little enough is known about the flux of a much-studied conserved quantity such as salinity (e.g., Walters et al. 1985). In the case of OC, we face additional difficulties due to the lack of data on spatial distribution. An inventory of STORET data, for example, performed in October 1979 yielded only 117 measurements of DOC and 506 measurements of TOC for the entire Bay-Delta region. More complete data are available for POC (Schemel and Dedini 1979), but, even there, sampling was confined to surface waters. In particular, the lack of vertically-averaged data on both carbon and velocity precludes estimation of mean advection of the mean organic carbon; the low frequency of measurements (*viz.*, less than 1 per tidal cycle) prevents understanding of diffusive flux; and the lack of data on vertical distribution prevents assessment of net flux relative to the estuarine circulation. All three processes can be significant for salt flux at the Golden Gate, for example.

Despite the inability to estimate exchange between subembayments or at the Golden Gate, some crude calculations can be used to illustrate the critical role of transport. First, we consider the ramifications of estuarine circulation on transport through the Golden Gate. Estuarine circulation induced by winter runoff causes a flow of bottom waters into the Bay from the coastal ocean, as clearly evidenced by long-term drifter movement (Conomos and Peter

1977). Peterson (1979) estimated oxygen exchange due to this circulation by assuming an average nontidal flow landward of 5 km d⁻¹ and seaward of 6 km d⁻¹ (Conomos 1975), each characterizing half the cross-sectional area at the Golden Gate. Based on the STORET data, the mean TOC value is 4.8 ± 0.2 (SE) mg l⁻¹ for the Bay-Delta. If we assumed a TOC value of 5 mg l⁻¹ for Central Bay and the flow rates used by Peterson (1979), the seaward losses would be 480 x 10⁹ g yr⁻¹, larger than any of the source terms considered previously.

Given these seaward losses, the *net* flux depends on the concentration of TOC in inflowing bottom waters. These concentrations are unknown. But for illustrative purposes, let us compare the net fluxes through the Golden Gate for two different TOC concentrations in bottom waters: 4 and 8 mg l⁻¹. In the first case, the landward flux would be 320 x 10⁹ g yr⁻¹, resulting in a net flux of 160 x 10⁹ g yr⁻¹ *seaward*; in the second case, the landward flux would be 640 x 10⁹ g yr⁻¹, resulting in a net flux of 160 x 10⁹ g yr⁻¹ *landward*. Both fluxes have large ramifications but in opposite directions -- for the carbon budget for Central Bay, as well as for the entire Bay. Clearly, ocean-Bay exchange is capable, in principle, of drastically modifying supply and loss rates for the estuarine pool of organic carbon.

A similar argument can be made for the potential importance of diffusive flux. Longitudinal diffusion coefficients have been assessed by several investigators, with estimates falling in the approximate range of 0.1-1 x 10⁶ cm² s⁻¹ (Conomos 1979, Table 4) and decreasing toward the Golden Gate in both the northern and southern reaches. A diffusivity of 0.4 cm² s⁻¹ and a gradient of 0.1 mg l⁻¹ km⁻¹ TOC through the Golden Gate would result in a flux of 11 x 10⁹ g yr⁻¹ due to mixing, comparable to estimates for benthic microalgal production in Central Bay. Peterson and his coworkers (Peterson et al. 1978; Peterson and Festa 1984) used a much higher mixing coefficient (4 x 10⁶ cm² s⁻¹) in order to simulate silica and phytoplankton distributions. Clearly, diffusive as well as advective fluxes may transport significant amounts of TOC between ocean and Bay, as well as between subembayments.

Some comments also can be made on the direction of net transport. The POC measurements of Schemel and Dedini (1979) suggest a gradient downward toward the Golden Gate for the northern reach (seaward of the null zone) and southern reach during winter, at least for data averaged over several years (Conomos et al. 1979, Fig. 9). If these measurements were representative of the entire water column -- and not just the surface waters where the samples were collected -- then the diffusive transport of POC should be seaward from all subembayments in winter. Indeed, a decrease in POC from estuary to coastal sea is common (Head 1976). In summer, on the other hand, average values were approximately the same from northern San Pablo Bay to below the San Mateo Bridge, with no clear gradient. On an annual basis, sediment budgets suggest a net transport of sediments from South Bay (Krone 1979). Similarly, Conomos et al (1979) describe a net transport of South Bay sediment from inflows and bottom resuspension to Central Bay, where it is deposited or released to the ocean. The sediment data may be considered weak evidence for similar behavior of POC. The existing data thus support a net seaward transport of POC.

A.4.2 Dredging activity

Dredging and dredged material disposal -- arguably a form of biotic transport, but treated separately here -- results in the transport of large quantities of sediment within and between subembayments, and between Bay and ocean. Currently, four open water dredge disposal sites exist: Alcatraz, San Pablo Bay, Carquinez Strait, and Suisun Bay (AHI and PWA 1990). The Alcatraz site is the only one to which material is transported from another subembayment, primarily South Bay. AHI and PWA (1990) tabulated annual average Federal dredging for the period 1975-1985, when a mean of $0.97 \times 10^6 \text{ m}^3$ was transported from South Bay to the Alcatraz site. A crude estimate of the organic carbon content can be determined by assuming a solids content of 34% (AHI and PWA 1990) and a mean TOC:dry wt. of 1.4% (Thomson-Becker and Luoma 1985). The implied movement of organic carbon amounts to $4.1 \times 10^9 \text{ g C yr}^{-1}$ using these approximations. During 1986-1987, 38% of the dredging was generated by non-Federal projects (AHI and PWA 1990). If we apply this same value to the period 1975-1985, then the organic carbon transported between South and Central bays would increase to $7.4 \times 10^9 \text{ g C yr}^{-1}$.

In view of the uncertainty in our assumptions, the transport could be considerably smaller or larger. The TOC data, for example, has an uncertainty range of 0.5-2% dry wt., and may also be spatially biased as samples were collected only from intertidal stations (Thomson-Becker and Luoma 1985). Furthermore, much of the material dumped at the Alcatraz site may consolidate and accumulate on the bottom. USCOE (cited by AHI and PWA 1990), for example, estimated that 38% of the material disposed at Alcatraz remained at that site as consolidated bottom material. A value of only $5 \times 10^9 \text{ g C yr}^{-1}$ is therefore used for 1980.

In San Pablo and Suisun bays, dredging activity results only in a redistribution of organic carbon, although the altered distribution may ultimately result in changes for other fluxes such as physical transport (AHI and PWA 1990).

A.4.3 Biotic Transport

Biotic transport, where it has been estimated quantitatively, almost always represents a net loss to the estuarine ecosystem. For example, Hopkinson and Day (1977) estimated a net faunal outmigration of $89 \text{ g dry wt. m}^{-2} \text{ yr}^{-1}$ for Barataria Basin, Louisiana. Similarly, Knox (1985) estimated a net migration loss of $4.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ fish and $0.13 \text{ g C m}^{-2} \text{ yr}^{-1}$ birds from the Upper Waitemata Harbour, New Zealand. Almost no quantitative data are available regarding biotic transport for San Francisco Bay, but there is little reason to believe that this estuary is an exception.

The northern anchovy (*Engraulis mordax*) is probably the most abundant species in the Bay as a whole, and probably in each of the three seaward subembayments as well. Although capable of spawning in the Bay, most spawning may actually take place out of the Bay. If this is indeed the case, then the anchovy is more likely a sink than a source for the Bay organic carbon pool.

the same could be deduced about any marine migrant that is also a saltwater spawner, using the estuary only as a nursery.

The Pacific herring (*Clupea harengus*), a marine migrant that is an estuarine spawner, provides one of the better-documented cases of biotic transport. Herring enter the Bay each year from late fall through winter to spawn along the western shores of Central Bay north of the Golden Gate. Although adults spend only a few months in the Bay, a large fraction of their biomass is deposited as eggs. Numbers have been increasing in recent years and the estimated 1989 population biomass was 71×10^9 g wet wt. (J. Spratt 1990, pers. comm.). Assuming that eggs constitute 22% of the biomass and that the C:wet wt. ratio is 0.15 for eggs, the 1989 population was carrying 2.3×10^9 g C of eggs. Up to 15% of the estimated population size can be harvested; the remaining fish and eggs are subject to intense predation by other fish, gulls, and sea lions. The young from surviving eggs feed in the Bay -- mostly Central and San Pablo Bays -- for 9 months before moving out to sea. The herring migration could result in a net gain in the estuary only if the biomass of deposited eggs and mortality in the estuary exceeded the emigration of surviving young and adults.

Certain anadromous species migrate from the sea through the estuary to upstream spawning areas. The adults die -- their carcasses may eventually contribute to riverine loading of organic carbon -- and the young move through the estuary back to sea. Some direct contributions to the estuarine organic carbon pool may occur through mortality during migration, but these are probably minor. For example, migrating chinook salmon (*Oncorhynchus tshawytscha*) number between approximately 70,000 and 500,000, with a typical wet weight of 5 kg. The equivalent organic carbon is only about 0.1×10^9 g C yr⁻¹ (Gulland 1970), which would have a minor effect even if all of it ended up in the estuary. Similarly, the biomass of migrating American shad (*Alosa sapidissima*) is probably between 0.1 and 1×10^9 g C yr⁻¹.

Other anadromous fish feed and grow within the estuary, not simply using it as a migration route. These species, such as striped bass (*Morone saxatilis*), are most likely a sink, transporting the accumulated biomass upstream to spawn.

No basis appears to exist for assessing biotic transport due to marine mammals or waterfowl in the Bay. The migratory biomass of marine mammals and the consequent effect they can have on TOC transport is likely to be even less than for fish populations. As far as waterfowl are concerned, the Bay-Delta is part of the Pacific Flyway and millions of birds feed on vegetation in the marshes. Their activity may very well increase the loading of organic carbon to estuarine waters. However, this contribution would fall into the category of tidal marsh export, not biotic transport, and presumably was included in the measurements from other estuaries on which we base our estimates of tidal marsh contributions.

A.5 ORGANIC CARBON SOURCES FOR INDIVIDUAL SUBEMBAYMENTS

A.5.1 Overview

A summary and comparison of the individual estimates for 1980 is informative, but certain caution must always be borne in mind. Estimates for several processes that may be important -- benthic microalgal productivity and tidal marsh export, for example -- have a large range of uncertainty, perhaps as large as an order of magnitude, that is, a factor of 10 ± 0.5 . These errors have been treated partially, but for the most part remain unquantified. Even when uncertainty ranges are specified, there is often no objective way to utilize them in comparing estimates. The probability of a given value within the uncertainty range is usually neither uniform nor Gaussian. Thus, the fact that two uncertainty ranges overlap implies that the two processes could be similar in magnitude, but indicates nothing regarding the likelihood. Nonetheless, these ranges do have value. First, when ranges for two processes truly do not overlap, we can conclude that the processes differ in magnitude. Second, uncertainty ranges make explicit the potential for error, even if the error cannot be specified quantitatively. The tendency to naively accept carbon budget estimates at face value is rampant in the scientific literature, leading to a premature acceptance of tenuous conclusions and poor management decisions. Finally, when uncertainty ranges are combined with the need for conservation of mass, analytical techniques can be used to determine if the underlying conceptual model and data are consistent (Klepper and Van de Kamer 1987). They also can be used to narrow the uncertainty ranges. This optimization approach requires estimates of all sources and sinks, something not possible within the constraints of the current report, but a worthy goal for the near future.

The estimates of the previous two sections provide some guidance as to conditions in 1980 (Table A.4). Several groups of processes can be distinguished, based on their percentage contribution to the known organic carbon sources of each subembayment, that is, excluding physical transport. Percentages were calculated under the assumption that only 10% of the TOC loading from Delta discharge is available (Sec. A.3.1). Sources other than Delta discharge were not corrected, due to the lack of data. However, the main sources in the Bay -- planktonic and benthic microalgal productivity -- are probably largely available to the food web, either through direct consumption or after transformation to detritus and bacterial biomass. It was thought that correction of the Delta loading alone, although seemingly inconsistent, would actually give a more accurate picture of food sources in the Bay than making uncertain assumptions about the availability of other sources, or making no adjustments at all:

(1) The first group consists of those processes that were almost definitely unimportant, based on their negligible contribution and a judgement that uncertainty ranges do not include nonnegligible contributions. This group includes seagrasses, photosynthetic bacteria, atmospheric deposition, spills, and runoff. They probably contributed a total of less than 10% in the case of each subembayment.

2) The second group consists of processes that also appear to be insignificant, but the evidence is anecdotal and the conclusion less certain. This group includes macroalgae, groundwater, and biotic transport.

Table A.4

Organic carbon sources for San Francisco Bay and its major subembayments (10^{11} g C yr⁻¹).

Carbon sources	SB	CB	SP	SU	SF	Year
Autochthonous						
Phytoplankton	0.71	0.15	0.39	0.05	1.30	80
Benthic microalgae ^a	0.32	0.11	0.12	0.02	0.57	80,85
Seagrasses	0.00	0.00	0.00	0.00	0.01	87
Macroalgae	n.s.	n.s.	n.s.	n.s.	n.s.	-
Photosynthetic bacteria	n.s.	n.s.	n.s.	n.s.	n.s.	-
Allochthonous						
Delta discharge	0.00	0.00	0.00	1.80	1.80	80
Tidal marsh export	0.05	0.00	0.10	0.06	0.21	85
Point sources	0.07	0.05	0.00	0.02	0.13	80
Runoff ^b	0.04	-	0.02	0.01	0.07	80
Atmospheric deposition	0.00	0.00	0.00	0.00	0.01	78
Spills	0.00	0.00	0.00	0.00	0.00	86
Groundwater	n.s.	n.s.	n.s.	n.s.	n.s.	-
Transport						
Circulation and mixing	?	?	?	?	?	-
Dredging ^c	0.00	0.05	0.00	0.00	0.00	75-85
Biotic transport	n.s.	n.s.	n.s.	n.s.	n.s.	-

Notes: Tidal marsh habitat is external to the system boundaries under consideration. Where applicable, epiphyte production is implicitly included with host plant production. Estimates are for the indicated year only. The uncertainty in some of these estimates is considerable and the text must be consulted for essential details. N.s. = probably not significant, but no quantitative evidence.

^aIntertidal habitat area based on 1985 data, subtidal on 1980 photic depth data.

^bCB included with SP.

^cAverage for 1975-1985.

(3) A third category consists of processes that contributed at least 10% in at least one subembayment, but never more than 25%. This group includes tidal marsh export, point sources, and dredging. These fluxes may have been significant secondary sources, but were probably not major sources, during 1980.

(4) The final group is composed of processes that were major sources (>25%) for at least one subembayment during 1980. Phytoplankton and Delta discharge belong to this category, and in fact each was the dominant source (>50%) for at least one subembayment. Benthic microalgal productivity was never dominant, but may have been a major source for South and Central bays. Physical transport may very well also be a member of this group.

The first two groups will be dropped from consideration in what follows. No evidence supports the notion that any of these processes are significant sources for the organic carbon pool, that they were notable in the past, or that they will be in the future (see Russell et al. 1982 for long-term trends in atmospheric deposition and runoff of BOD₅; and Silverman et al. 1983 regarding short-term trends in runoff of hydrocarbons). Even if all other sources in each subembayment were to drop by a factor of ten, these processes would still account for less than half of the organic carbon supply. Considering the paucity of data on processes such as atmospheric deposition, and the interannual variability in processes such as runoff, the significance of the above sources cannot be ruled out with assurance. On the other hand, they must be considered of lower priority in trying to understand the supply of energy to the food web.

Ignoring physical transport for the moment and standardizing on the basis of unit area, South, Central, and San Pablo bays have similar annual carbon supplies -- $3 \times 10^2 \text{ g C m}^{-2} \text{ yr}^{-1}$ for South Bay, and $2 \times 10^3 \text{ g C m}^{-2} \text{ yr}^{-1}$ for both Central and San Pablo bays. If we estimate "available" carbon loading from Delta discharge into Suisun Bay on the basis of BOD (See A.3.1), then Suisun Bay also has a carbon supply of $3 \times 10^2 \text{ g C m}^{-2} \text{ yr}^{-1}$. These values are within the surprisingly small range of 150-400 $\text{g C m}^{-2} \text{ yr}^{-1}$ characteristic of temperate North American estuaries (Nixon 1981a). Except for Suisun Bay, almost all of the known carbon supplies -- that is, not accounting for physical transport -- are currently autochthonous.

We now turn to a consideration of each subembayment, in an effort to further understand the mixture of organic carbon sources in 1980 and the effects of year-to-year fluctuations on the mixture.

A.5.2 South Bay

Conditions in 1980. The dominant energy source for the South Bay food web in 1980 appears to have been phytoplankton productivity (Table A.4). Benthic microalgal productivity could also have been a major source, although the uncertainties inherent in both estimates preclude a more quantitative or more certain conclusion. Tidal marsh export, even allowing for studies that suggest export fluxes can be a factor of three higher, and even assuming a high

availability, was probably small compared to autochthonous productivity. The role of circulation and mixing as a direct organic carbon source is unknown, although physical transport probably acts as a net sink for South Bay POC (Sec. A.4.1). The remaining known sources were almost definitely unimportant, even within their respective ranges of uncertainty.

Interannual variability. Net photic zone productivity P_{np} has been estimated for the channel of South Bay for the period 1980-1987 (Cloern 1990; Fig. A.4). There was no apparent trend in annual production. Although peak productivity varied markedly from one year to the next, the fluctuations in annual production were small. The coefficients of variation (CV) during this period were 26% for annual mean P_{np} and 28% for annual mean volumetric biomass b . The maximum (in 1983) was only about twice the minimum (in 1987) for both productivity and biomass.

A comparison of NWI habitat maps for 1958 and 1985 show a decrease of only about 1% in mudflat area and 10% in tidal marsh area during that period. No evidence, therefore, exists to suggest recent significant trends in either benthic microalgal productivity or tidal marsh export of organic carbon. The absence of long time series for benthic microalgae productivity or tidal marsh export, however, precludes a convincing assessment of interannual changes. Major decreases in tidal marsh did take place between 1850 and 1958 (Atwater et al. 1979), and tidal marsh export could have been a dominant organic carbon source in the nineteenth and early twentieth century.

Point source discharge is the only source with a detailed record for the years prior to 1980. The decrease has been quite remarkable (Fig. A.5), particularly since 1972 when the Federal Clean Water Act required a minimum of secondary treatment for all dischargers. The peak load in 1965 was almost exactly 10 times the 1985 load; the corresponding "available" TOC was probably about 0.3×10^{11} g C, the same as the 1980 estimate for benthic microalgal production. In view of the interannual variability in phytoplankton productivity, municipal wastewater could have been one of the dominant organic carbon sources for the South Bay during the 1960s and early 1970s, at least for years when microalgal activity was low. It is clear from Table A.4 and Fig. A.5, however, that point source discharge no longer plays a large role in the organic carbon supply for South Bay as a whole.

For certain regions contained within South Bay, the role of wastewater, both past and present, may be more notable. The area south of the Dumbarton bridge, for example, experienced an even larger decrease in BOD loading -- about 15-fold between 1960 and 1985 -- than the South Bay as a whole (CRWQCB-SFBR 1987). Sewage loading per unit area was 2.6 times higher in this region in 1985, and both the current role of point sources, as well as the consequences of the decrease since 1960, are probably more important. Separate estimates for phytoplankton productivity and other processes in this zone are not available, however, for comparison.

Mechanisms of interannual variability. Assuming that the South Bay food web is now driven primarily by energy from phytoplankton and, perhaps, benthic microalgae, the controls

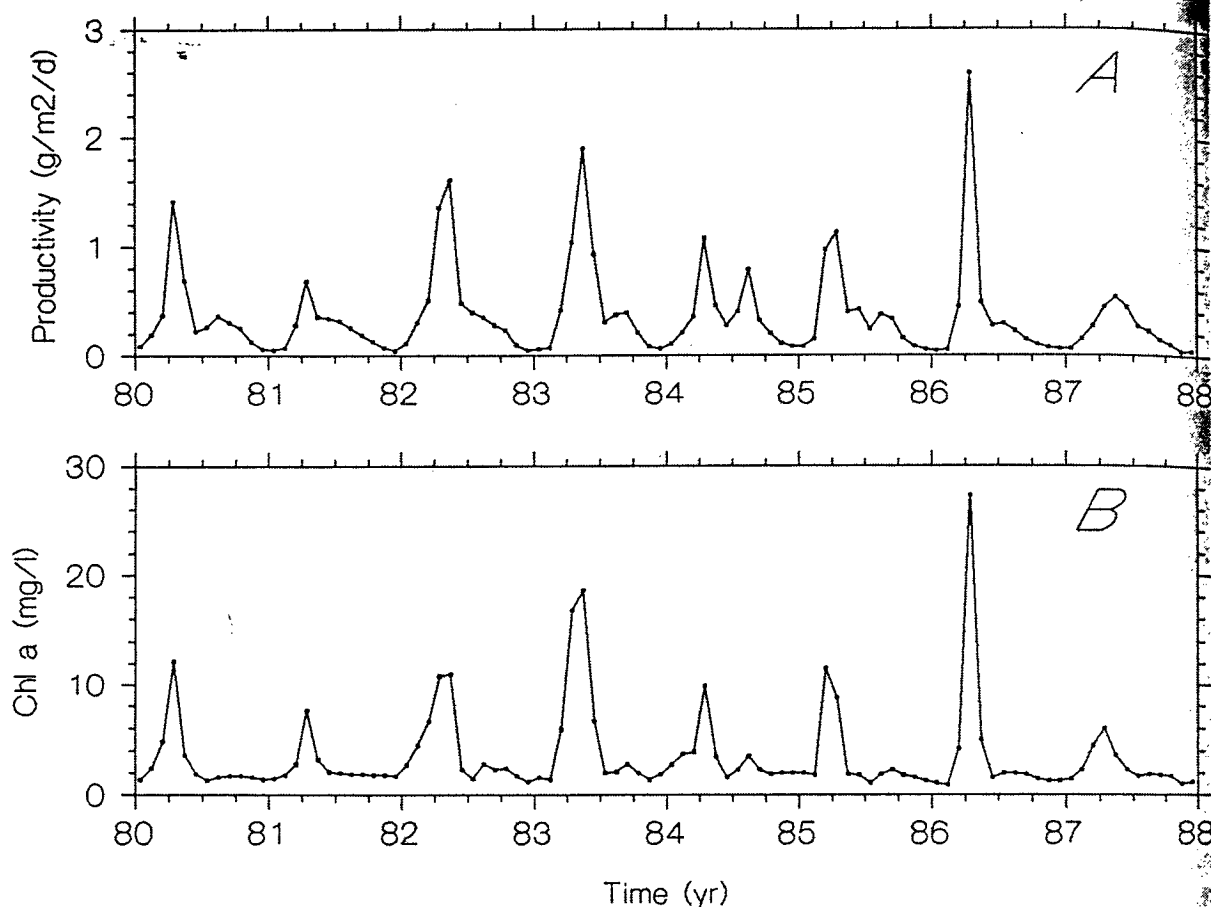


Figure A.4 Monthly mean values for (A) photic zone productivity and (B) biomass in the channel of South Bay between USGS stations 24 and 30 (data from USGS).

on year-to-year fluctuations in primary productivity are of great interest. Nutrient concentrations typically exceed levels that limit phytoplankton growth rates and are thus not a factor (Conner et al. 1979). In the absence of nutrient limitation, both net water column productivity P_{nw} ($\text{g C m}^{-2} \text{ d}^{-1}$), as well as net photic zone productivity P_{np} , can be shown to depend on three quantities, aside from intrinsic physiological variables: surface irradiance I_0 ($\text{E m}^{-2} \text{ d}^{-1}$), the ratio of photic to mixing depth Z_p/Z_m , and areal phytoplankton biomass B ($\text{mg m}^{-2} \text{ Chl } a$). This empirical result is true of San Francisco Bay and many other estuaries (Cole and Cloern 1987; Cloern 1987). Assuming a well-mixed water column, it also can be derived from simple theoretical considerations, similar to those discussed by Platt (1980). Understanding variability in P_{nw} is equivalent, then, to understanding what controls surface irradiance I_0 , the depth ratio Z_p/Z_m , and biomass B .

Cloern (1979, 1982, 1984) and Cloern et al. (1985) hypothesized a mechanism contributing to interannual variability in South Bay that acts through the depth ratio and biomass.

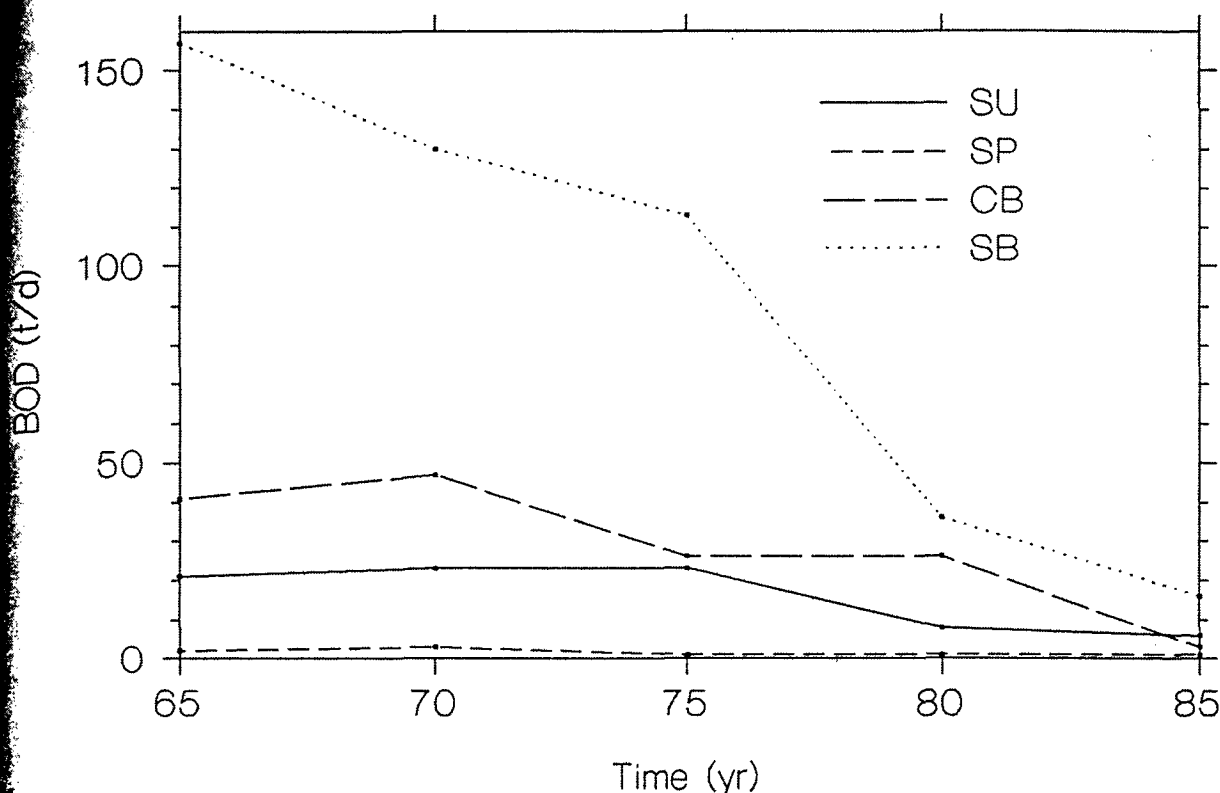


Figure A.5 Five-day BOD loading from municipal wastewater for the major subembayments of San Francisco Bay (data from CRWQCB-SFBR [1987]).

Specifically, when periods of high Delta discharge in winter-spring coincide with periods of low tidal current speed during the tidal cycle, South Bay waters stratify. Apparently, the buoyancy flux from freshwater inflow dominates the dissipation of kinetic energy by tidal mixing at these times. The mixed layer Z_m becomes smaller, which alone would increase the depth ratio. In addition, however, heavier suspended particles sink out of the stable surface layer and turbidity decreases, resulting in a deeper photic depth Z_p and an even larger increase in the depth ratio. The result is an increase in the doubling rate in the mixed layer. Phytoplankton in the mixed layer also become effectively isolated from benthic mollusks, polychaetes, and other suspension feeders, which are capable of filtering the entire water column daily. Phytoplankton biomass is thus released from the constraints of a severe loss process. Although mixed-layer productivity is offset during stratification by respiratory losses below Z_m , it can be shown that the mixed-layer gains will dominate very quickly. The combination of higher Z_p , lower Z_m , and reduced grazing drain on B thus leads to rapid accumulations of biomass and much higher productivity.

If this mechanism were indeed an important source of interannual variability, we would expect to see a relationship between annual phytoplankton productivity in South Bay and some relevant aspect of Delta discharge. Cloern (1990) provided some evidence along these lines,

using estimates of net photic zone productivity in the channel for the period 1980-1987. Specifically, estimated February-May productivity in the photic zone was correlated with January-April river flow ($p < 0.025$). The statistical evidence, combined with the plausible mechanism outlined previously, supports the hypothesis that river discharge contributes to interannual variability of phytoplankton productivity in South Bay.

Although freshwater flow appears to play a role, the nature and magnitude of the role bears further study. The linear relationship between discharge and productivity accounted for 65% of the variability; a large proportion of the variability remains unexplained, implying that other factors may have an important influence. In particular, the function of local flows directly into South Bay needs attention (J. Cloern 1990, pers. comm.). These flows are sometimes large and they could influence productivity through the same mechanism as Delta discharge, and they could be confounded with the latter.

The analysis, moreover, was based on net photic zone productivity, not net water column productivity. Biomass is highly correlated with net water column productivity, whether for the entire year ($R^2 = 0.79$, $p < 0.01$) or the February-May period ($R^2 = 0.83$, $p < 0.01$). Consequently, respiratory losses below the photic zone are probably higher when P_{np} is higher and the variability in net water column productivity is probably lower than net photic zone productivity. It is the former quantity, however, that is of main interest, as it represents the energy available to primary consumers.

Finally, 50% of South Bay is shallower than 2.2 m below MLLW (Table A.1). Over 60% of the annual phytoplankton production takes place in shoal areas, defined here as extending to 2 m below MLLW (Table A.3). The relevance of the productivity time series, which was based on data collected at channel stations, is unknown for these shoals. Certainly, the responses of South Bay shoal and channel habitat to mixing forces are different (Powell et al. 1989). Also, the proposed mechanism relating stratification to increased productivity could be inapplicable to shoal areas, which probably do not stratify. Both Z_m and access to phytoplankton by benthic herbivores in the shoals may thus remain unaffected by Delta discharge. Suspended particulate matter (and thus Z_p) and B are still free to respond to Delta discharge and other forces (Cloern et al. 1989). However, the dominant mechanisms underlying fluctuations in these variables and the consequences for annual phytoplankton productivity in shoal regions have not been delineated adequately. In addition to Delta-derived intrusions of turbid water, local streams and runoff and resuspension of sediments may play a role in modulating Z_p (Conomos et al. 1979). Resuspension of chlorophyll (Thompson et al. 1981) also may contribute to variability in B . As resuspension probably decreases Z_m and increases B , the net effects on phytoplankton productivity are particularly hard to assess.

The same phenomena that affect phytoplankton productivity in the shoals can be expected to modulate benthic primary productivity, although not necessarily in the same direction. Resuspension, for example, probably decreases both benthic biomass and the light energy incident on the benthos, resulting in depressed benthic microalgal productivity. Although various

influences such as resuspension can be described qualitatively, their actual significance has not been measured.

Implications for the near future. As previously mentioned, annual mean P_{np} in the channel had a CV of 26% for the period 1980-1987. If P_{nw} were considered instead of P_{np} , and the variability of shoal areas was included, the apparent year-to-year fluctuations in primary productivity of South Bay could be even less. In contrast, annual Delta outflow (DAYFLOW method) during this period had a CV of 81%, with a maximum more than 13 times the minimum. Thus, even if Delta discharge does underly interannual variability of primary production in South Bay, the effects of river outflow are heavily damped. Annual production appears to be relatively stable.

The recent appearance of the Asian corbulid clam *Potamocorbula amurensis* (Carlton 1990) introduces a new element of uncertainty, particularly for South Bay south of the Dumbarton Bridge. *Potamocorbula* is currently present, but not abundant, in South Bay both north and south of the Bridge (Carleton 1990). According to a synoptic survey in 1973 (Nichols 1979; Thompson and Nichols 1981), benthic invertebrate biomass south of the Bridge was 50% less than biomass north of the Bridge in summer, 80% less in winter. Organic carbon sources have not yet been tallied for the lower South Bay independently. Little reason exists, however, for expecting a lower food supply, particularly as tidal marsh export, point source discharge, and runoff are probably much higher here than for South Bay as a whole. A potential may be present for higher benthic biomass, increased grazing pressure, lower phytoplankton biomass, and reduced phytoplankton productivity. *Potamocorbula* perhaps can exploit this opportunity because of its apparent ability to withstand a much wider range of sediment types and salinity than other benthic macroinvertebrates (Carleton 1990). In South Bay north of the Dumbarton Bridge, on the other hand, benthic biomass is more typical of intertidal communities (e.g., Knox 1986b). *Potamocorbula* may very well displace certain members of the current estuarine invertebrate community, but the total biomass and consequent grazing pressure may not change dramatically. Note that interannual variability is high among the benthos, despite the absence of long-term trends (Nichols and Thompson 1985b); thus, the applicability of the 1973 data to subsequent years is actually unknown and the suggestions made here highly speculative.

A.5.3 Central Bay

Boundaries for the central basin. Central Bay has often been partitioned into a southern portion, which is regarded as part of "South Bay," and a northern portion, which is regarded as part of "North Bay." Topographic considerations, however, suggest that the central portion should be considered separately, as evidenced by the hypsographs of Fig. A.2. The most informative boundaries for "Central Bay" are not necessarily those delineated by the AHI segmentation scheme. In particular, the region between the San Bruno shoal and the Bay Bridge may have less affinities with the rest of South Bay than with what we have been calling Central Bay (cf. Powell et al. 1986). This point is illuminated further by examining the few relevant time series that exist. From late 1977 through 1980, chlorophyll *a* was measured almost monthly

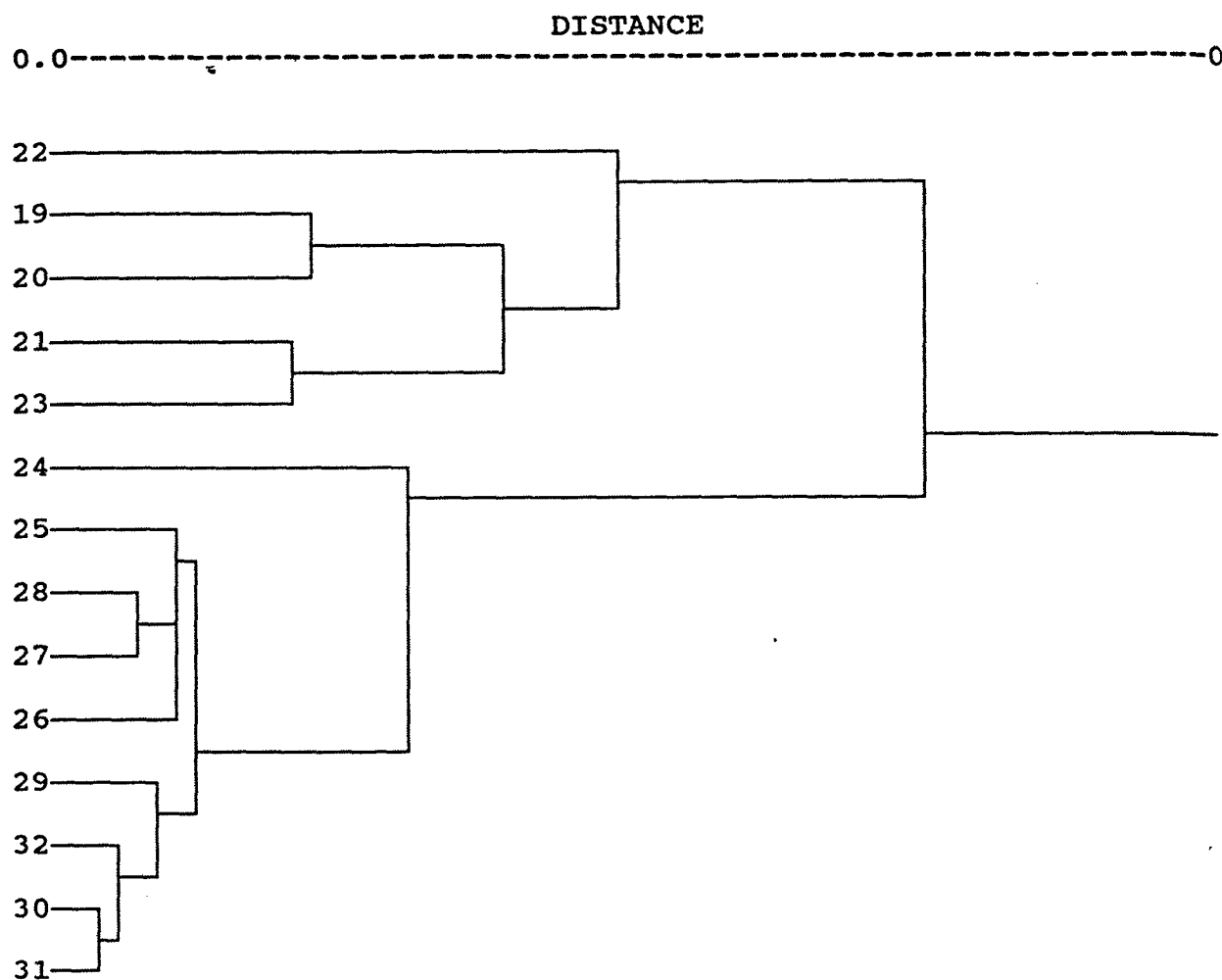


Figure A.6 Tree diagram for Central and South Bay USGS stations 19-32, based on monthly mean chlorophyll for Nov 1977-Dec 1980 (data from USGS).

at 14 channel stations from the Golden Gate down through the South Bay (J. Cloern 1990, 1 comm.). A cluster analysis (nearest-neighbor, Pearson metric) based on monthly mean chlorophyll *a* for these stations revealed a tight grouping south of the San Bruno shoal (USGS station 24) and a second affiliation of stations from north of the shoal to the Golden Gate (Figure A.6). The northern group of stations was more loosely clustered, indicating higher spatial heterogeneity. The San Bruno shoal itself was a transition region, but it had higher affinity to the tight cluster to the south. This southern group could be further subdivided by the San Mateo Bridge (USGS station 29) into a "tight" southern cluster and a "looser" northern cluster. The results of the cluster analysis are quite consistent with studies of zooplankton distribution (Ambler et al. 1985) and mesoscale chlorophyll variability (Powell et al. 1986). Unfortunately because of the way the Bay has been subdivided for reporting past studies, it was not possible here to delineate carbon sources within these perhaps more meaningful boundaries.

Conditions in 1980. Central Bay -- as defined by the AHI segmentation scheme -- was dominated by phytoplankton and benthic microalgal productivity in 1980, at least as far as the "known" carbon sources were concerned (Table A.4). Point sources and dredging contributed significant amounts, but were almost definitely of secondary importance.

The flux of organic carbon from both South and San Pablo bays is unknown and could very well have been a significant source. The longitudinal profile of annual mean chlorophyll in 1980 suggests transport of chlorophyll into Central Bay from San Pablo Bay and from South Bay, at least from south of the San Bruno shoal (Cloern 1987, Fig. 4). As discussed previously, the winter gradient of surface POC also suggests transport into Central Bay from both adjoining subembayments, but the summer gradient is less certain (Conomos et al. 1979).

The coastal ocean also may have functioned as a net source of chlorophyll and possibly POC. In 1980, the annual mean extinction coefficient decreased toward the Golden Gate and, as a result, estimated annual productivity reached a Central Bay maximum at this boundary with the coastal ocean (Cloern 1987). It is thus possible that the lower extinction coefficient and, perhaps, decreased benthic grazing pressure compensated for the higher mixing depth. Annual net productivity may have actually been higher just outside the Golden Gate. If higher productivity were reflected in higher biomass accumulations, then the net chlorophyll flux could very well have been into the Bay. On an annual basis, the mean chlorophyll gradient is uninformative, however; the gradient within Central Bay is very weak, from the boundary with San Pablo Bay down to the San Bruno shoal.

Interannual variability. Whatever the exact boundaries that best further understanding, the central basin has been relatively overlooked both in long-term biological sampling and in delineation of causal mechanisms. In particular, no long-term chlorophyll series exist to adequately characterize interannual variability of either phytoplankton or benthic microalgae.

As in South Bay, wastewater discharge must have been a significant source of organic carbon in the recent past. Peak values occurring in 1970 (Fig. A.5) were equivalent to 0.1×10^{11} g yr⁻¹ of "available" TOC. This value is comparable to both estimated phytoplankton and benthic microalgal productivity, especially when we recall that the latter two processes have uncertainty ranges of at least 50% (Table A.4). Point source discharges no longer appear to play an important role in the carbon budget of Central Bay.

Transport associated with dredging exhibits high interannual variability (AHI and PWA 1990). The quantity moved from South Bay to the Alcatraz site in 1987, for example, was about twice the 1986 amount. Because dredging transport appears to be a secondary source of organic material, the interannual variability probably has little direct effect on the supply of organic carbon to the Central Bay food web. In the absence, however, of long-term data for the dominant processes -- phytoplankton and benthic microalgal productivity -- a role for dredging during certain years cannot be ruled out with assurance.

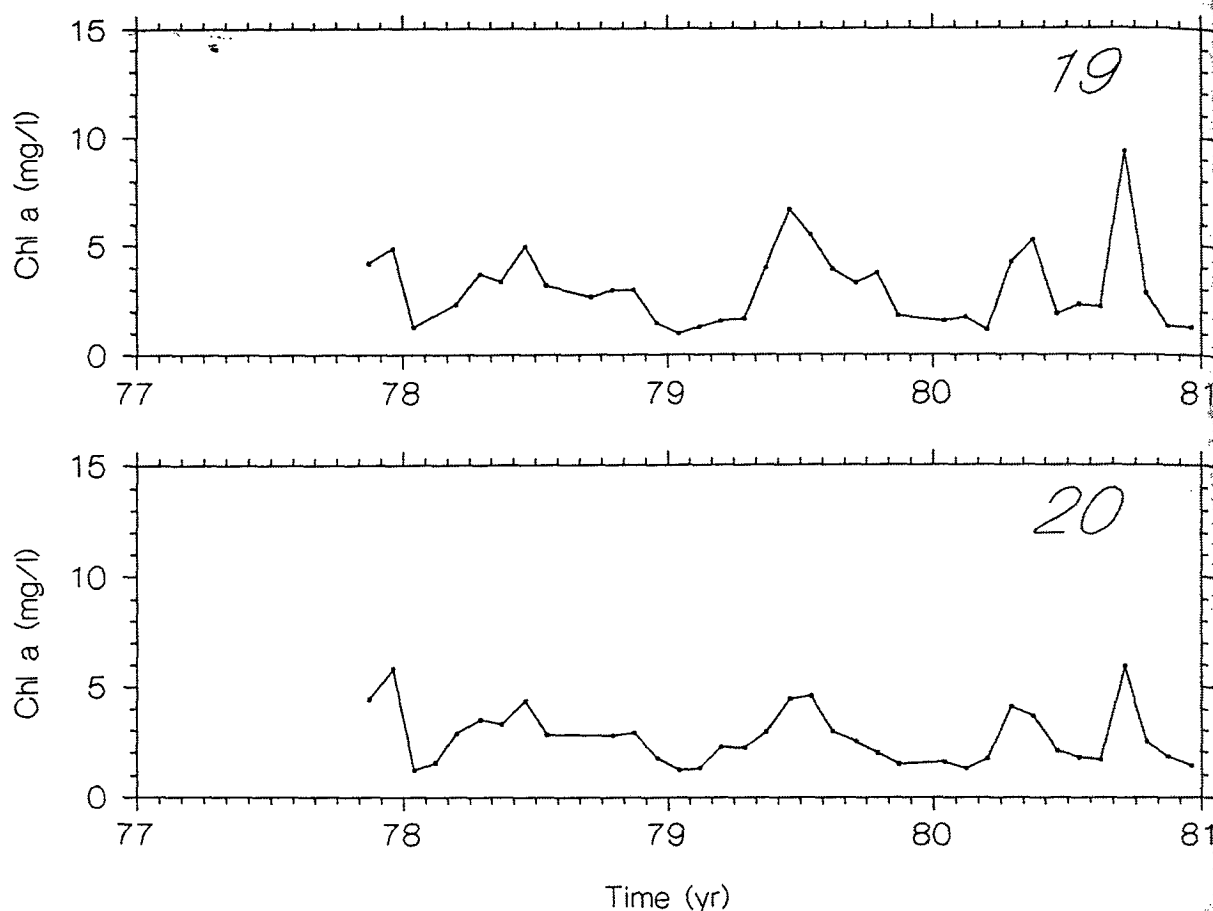


Figure A.7 Monthly mean chlorophyll *a* at Central Bay USGS stations 19 and 20 (data from USGS).

Mechanisms of interannual variability. Based on the cluster analysis described above and the likelihood of imports from adjoining subembayments and the coastal ocean, one would expect the mechanisms to be very different from South Bay proper. The 1977-1980 data for central basin USGS stations 19 and 20 allow a finer appreciation of this point (Fig. A.7). A chlorophyll pulse occurred in December 1977, for example, dominated by *Nitzschia seriata*, a neritic diatom which suggests an influx through the Golden Gate of a coastal bloom (Cloern 1979). Major biomass peaks for 1978-1980 occurred in May-June and sometimes in September-October at these stations. In contrast, South Bay stations have earlier biomass peaks slightly lagging Delta discharge (Cloern 1990); in 1980, for example, South Bay chlorophyll attained a single maximum in early April (Cloern et al. 1985). Although San Pablo Bay exhibits biomass peaks during May-June as well, the fall peak in Central Bay appears to be disconnected from the adjacent subembayments (Ambler et al. 1985, Fig. 2D). This difference in seasonal pattern between embayments suggests that the nature and causes of interannual variability differ as well. Unfortunately, the available data allow only inconclusive speculation, in the case of both phytoplankton and benthic microalgal productivity.

A.5.4 San Pablo Bay

Conditions in 1980. Phytoplankton productivity was also probably the dominant energy source for the San Pablo Bay food web in 1980 (Table A.4). Benthic microalgal productivity could have been a significant secondary source, but appears to have been relatively less important than in South or Central bays. Tidal marsh export was estimated to be the same magnitude as benthic primary productivity, but was relatively more important than in South and Central bays. Point sources were unimportant. As usual, the amount of organic carbon transferred from other subembayments was unknown but possibly significant.

Interannual variability. As in Central Bay, interannual variability of phytoplankton activity is difficult to characterize and to understand because of the paucity of long-term chlorophyll or productivity measurements in San Pablo Bay. During 1971-1973, chlorophyll samples were collected from both shoal and channel sites, but routine sampling has since been confined to channel sites near the Pinole shoal area (D42 until 1980, D41 since 1980; Ball 1987a). It is particularly unfortunate that no long-term data series are available for the shoals, as a majority of annual phytoplankton production probably takes place in the shallower region (Table A.3). Based on the study of seasonality during 1980 (Cloern et al. 1985) and the chlorophyll data that do exist for San Pablo Bay (Ball 1987a), interannual variability of phytoplankton has been attributed to processes similar to those of Suisun Bay. Much more data is available for Suisun Bay, so we defer the discussion of this variability to the following section.

Tidal marsh habitat area for San Pablo Bay may have undergone a larger reduction in recent decades than for South Bay (Atwater et al. 1979). The importance of tidal marsh export in the recent past hence may have been higher than in 1980 or later years. Unfortunately, the NWI habitat data for 1958 have not been digitized for San Pablo or Suisun bays, rendering a comparison with the 1985 data impossible at this time.

Point source discharge has never been important, even in 1970 when it peaked at a BOD load equivalent to $0.01 \times 10^{11} \text{ g C yr}^{-1}$ (Fig. A.5).

A.5.5 Suisun Bay

Conditions in 1980. Suisun Bay departs from the other subembayments in terms of organic carbon sources (Table A.4). For the others, phytoplankton productivity was the dominant, or at least a major, known source in 1980, with a possible major role for benthic microalgal productivity in South and Central bays. Benthic microalgal productivity also played a significant role in San Pablo Bay. In contrast, the dominant organic carbon source for Suisun Bay may very well have been Delta discharge; it appears to have dominated even if we consider only 10% to have been available to the food web of Suisun Bay (Sec. A.3.1; but see Sec. A.6). Phytoplankton productivity was of secondary importance. Tidal marsh habitat area may have decreased between 1980 and 1985, the year for which export estimates were made, but even the

data for 1985 implies that tidal marsh export rivalled and perhaps even exceeded phytoplankton productivity. In contrast to the other subembayments, benthic microalgal production appears to have been minor, as do point sources. Physical transport of organic material from San Pablo Bay may be mediated by gravitational circulation, but quantitative estimates of transport do not exist.

Two additional pieces of evidence support the view that phytoplankton productivity is not a dominant organic carbon source for Suisun Bay. First, the stable isotope results of Spiker and Schemel (1979) suggest that most POC in the entrapment zone (see below) may at times be of riverine origin. Second, bacterioplankton productivity at channel stations in Suisun Bay can greatly exceed phytoplankton productivity (J.T. Hollibaugh and P.S. Wong, pers. comm. 1991) suggesting that significant alternative sources of labile organic matter are present in the subembayment.

Of all the subembayments, tidal marsh export appears to have the greatest potential role in Suisun Bay, for several reasons. First, recall that the upper range for TOC export -- not including possible export of reduced sulfur -- is a factor of three higher than the estimated export. Its uncertainty range thus overlaps estimates of pigment-related carbon, POC, and "available" TOC loading from river flow in 1980 (Sec. A.3.1). Second, the morphometric characteristics of Suisun Bay tidal marsh may facilitate tidal exchange of materials with the open water. In particular, based on NWI map data, the ratio of tidal channel to vegetated tidal marsh is only 1% for both South and San Pablo bays, while it exceeds 7% for Suisun Bay. One might expect a correspondingly larger export flux for Suisun Marsh. Finally, operations in the marsh include periodic flushing of duck ponds and their ample organic matter stores, which may enhance marsh export of organic carbon, although the quantitative importance remains unknown.

As discussed previously, the availability of organic carbon exported from tidal marsh is a mystery. The stable isotope work of Spiker and Schemel (1979) is sometimes cited as evidence that tidal marsh export is insignificant in San Francisco Bay. These authors actually claimed merely that "detritus originating from *Spartina* marsh grass... was not identifiable as an important carbon source" in South Bay. This claim is consistent with the results for South Bay summarized in Table A.4, but several points should be noted in regard to the northern reach. First, the data consisted of only four channel transects, three of them during the 1976-1977 drought, and included no sediment samples for the northern reach. Second, the interpretation of single isotope studies with $\delta^{13}\text{C}$ is ambiguous for a number of reasons, particularly when several possible isotope sources are present and the sample has intermediate isotopic values (Peterson and Fry 1987). Third, as noted in a previous section, marsh export may be in the form of reduced sulfur autotrophic sulfur bacteria have a range of $\delta^{13}\text{C}$ values encompassing riverine, estuarine, and most marine phytoplankton values (Peterson et al. 1980; Fry and Sherr 1984). Clearly additional stable isotope studies of San Francisco Bay are necessary if any definitive conclusion regarding marsh export are to emerge from this method.

Interannual variability. Although interannual changes in riverine TOC loading cannot be evaluated, data do exist for an assessment of year-to-year fluctuations in the pigment-related carbon carried by Delta outflow. As discussed previously, carbon associated with chlorophyll

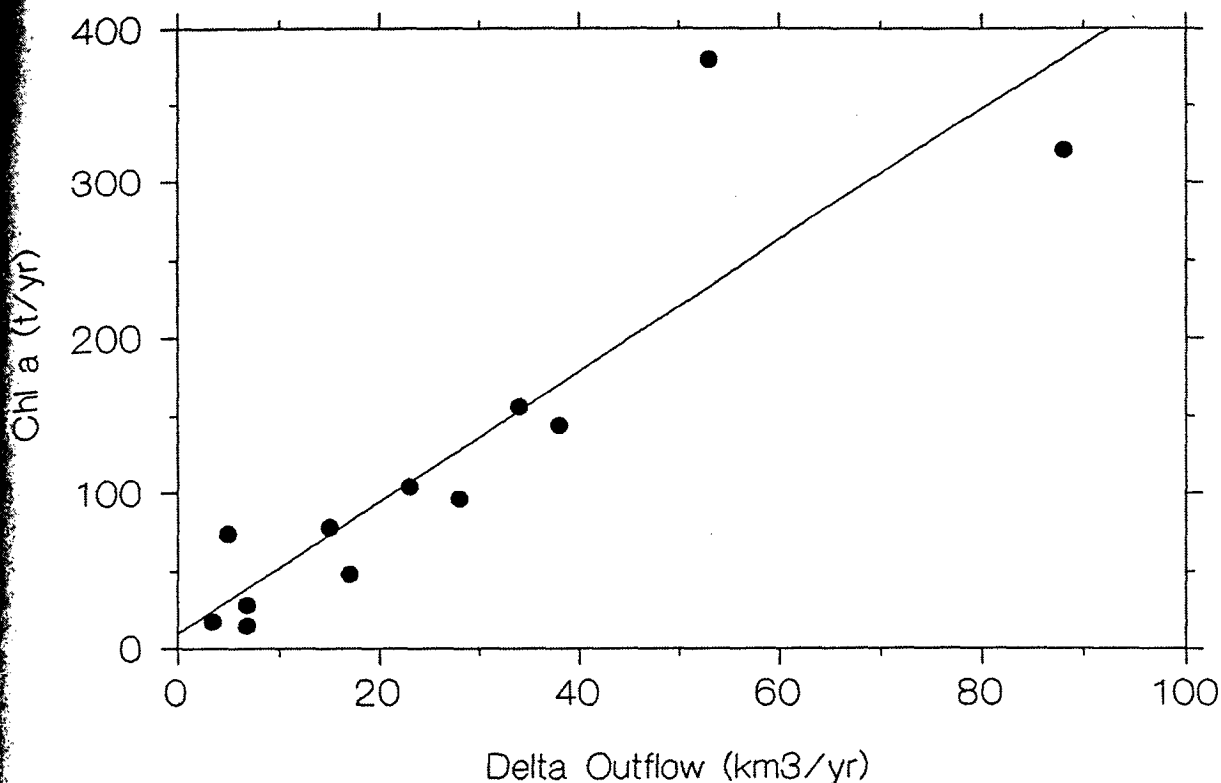


Figure A.8 Chlorophyll *a* loading, based on measurements from surface waters near Pt. Sacramento (D4), from 1976-1987 (data from DWR).

and its degradation products may account for much of the POC loading, and these materials may constitute most of the TOC loading actually available for consumption. Chlorophyll concentrations near the juncture between Suisun Bay and the Sacramento River at Point Sacramento (D4), combined with Delta outflow values, were used to estimate a flow-weighted loading of chlorophyll into Suisun Bay for 1976-1987. Loading of chlorophyll into Suisun Bay was strongly related to flow (Fig. A.8). In other words, the year-to-year fluctuations in riverine loading largely reflect the corresponding variability in Delta outflow. The current drought period that began in 1987, in particular, is probably a time of highly reduced chlorophyll loading from Delta outflow.

Part of the BOD load carried into Suisun Bay can be attributed to upstream point source dischargers (Sec. A.3.1). In the early 1970s, this load amounted to at least $14.4 \times 10^9 \text{ g yr}^{-1}$ BOD₅, falling off to 3.2×10^9 in 1979 (Hansen 1982). The significance of the decrease during the 1970s is uncertain. The estimates are minimum values and the actual decrease in point source discharge may have been much higher; on the other hand, much of the TOC in discharge may have been respired before reaching Suisun Bay. The BOD₅ from the Chipps Island station (D10) is informative, as it covers this time period approximately (Fig. A.9). No trend is apparent in this series, suggesting that upstream changes in municipal wastewater discharge did not affect

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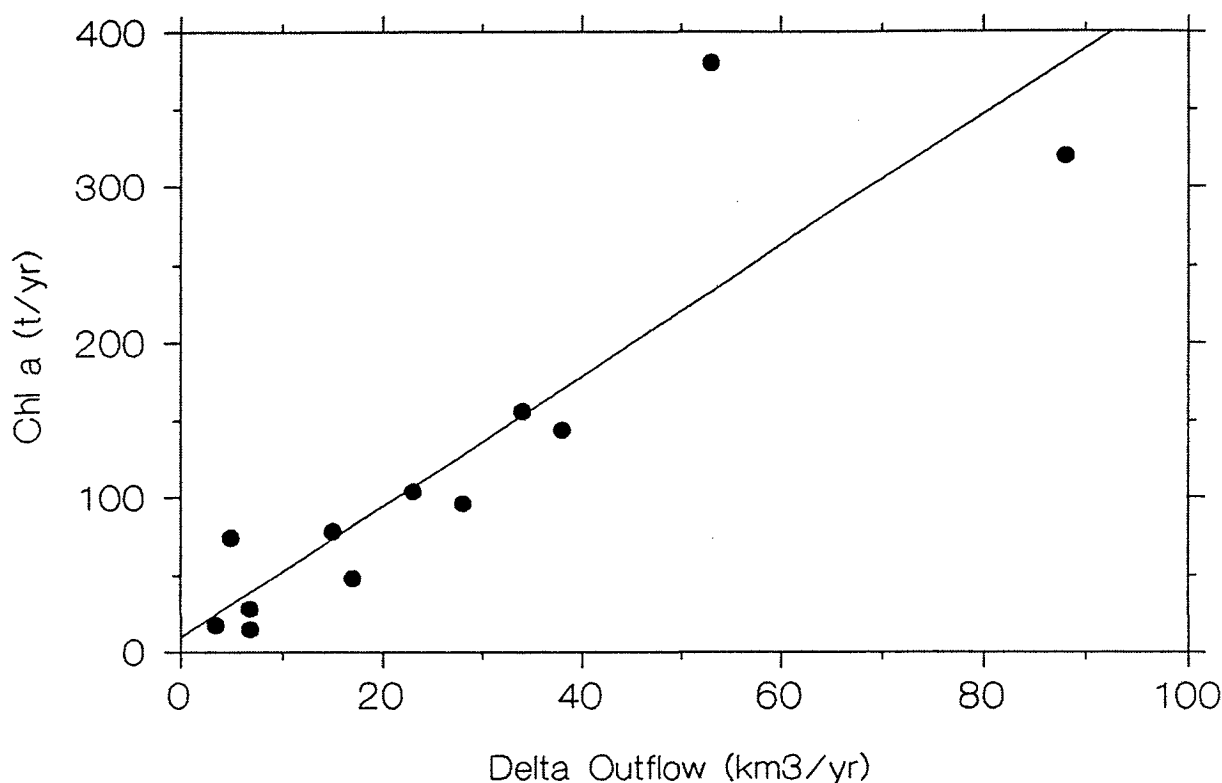


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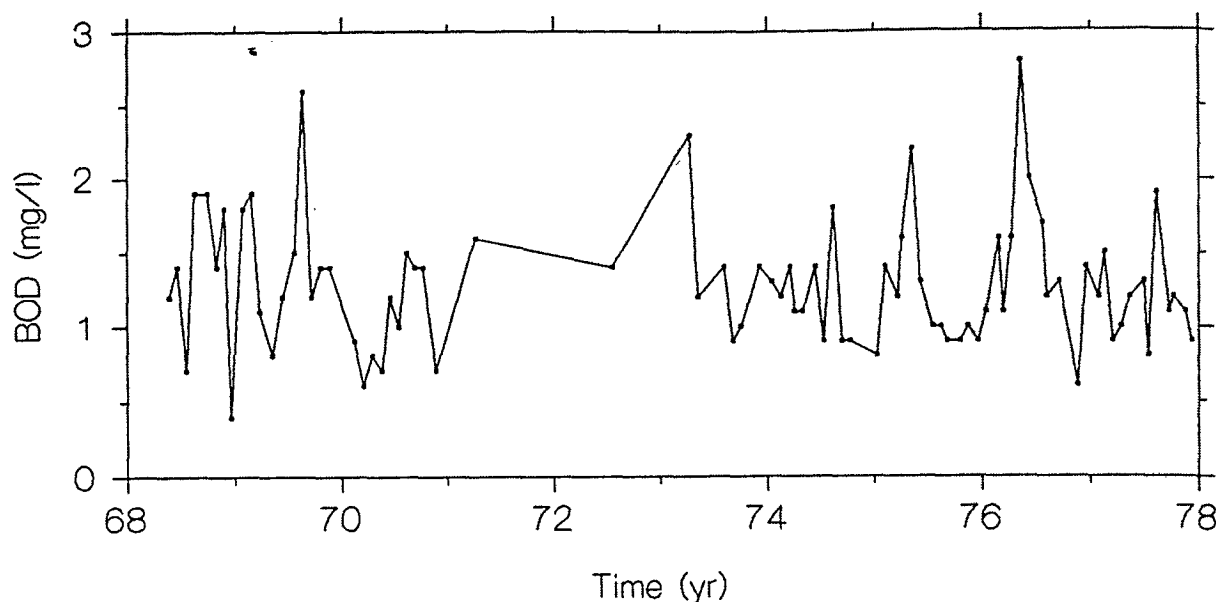


Figure A.9 Five-day BOD values measured in surface waters at a station near Chipps Island (D10; data from DWR).

the TOC loading to Suisun Bay. The evidence is not conclusive, however, as the Chipps Island station is subject to influences from within Suisun Bay as well as from Delta discharge. Note also that the BOD₅ pool does not necessarily reflect the rate of BOD₅ loading. Unfortunately, long BOD series from upstream sites do not exist.

Primary productivity measurements in Suisun Bay were repeated during 1988, a "very dry" year (Delta discharge of 4.7 km³), permitting a fruitful comparison with the data of 1980, an "intermediate" year (A. Alpine and J. Cloern 1990, pers. comm.). Productivity during 1988 was much lower than in 1980; net annual photic zone productivity π_{np} fell by a factor of five at shoal and channel stations. The drop in π_{nw} , which is simply π_{np} corrected for aphotic respiration (Sec. A.2.1), was probably smaller but nevertheless substantial. This decreased productivity was due to lower phytoplankton biomass, not lower growth rates.

Phytoplankton productivity in Suisun Bay -- even more so than for the other embayments -- is overwhelmingly dominated by shoal productivity (Table A.4). The 1980 data, for example, imply an annual phytoplankton productivity π_{nw} of 5.2×10^9 g C yr⁻¹ in the shoals, compared to a negative value of -0.48×10^9 g C yr⁻¹ in the channel (Table A.3). Interannual variability in embayment productivity must therefore reflect fluctuations in shoal, not channel, productivity. The decrease in productivity between 1980 and 1988 was largely attributable to biomass changes and not to a change in photic depth (which actually increased in 1988) or insolation (A. Alpine and J. Cloern 1990, pers. comm.). If biomass is generally the controlling factor for productivity in Suisun Bay, it follows that shoal biomass fluctuations should be a guide to variability in embayment productivity. In particular, the long-term data for chlorophyll *a* at a Grizzly Bay

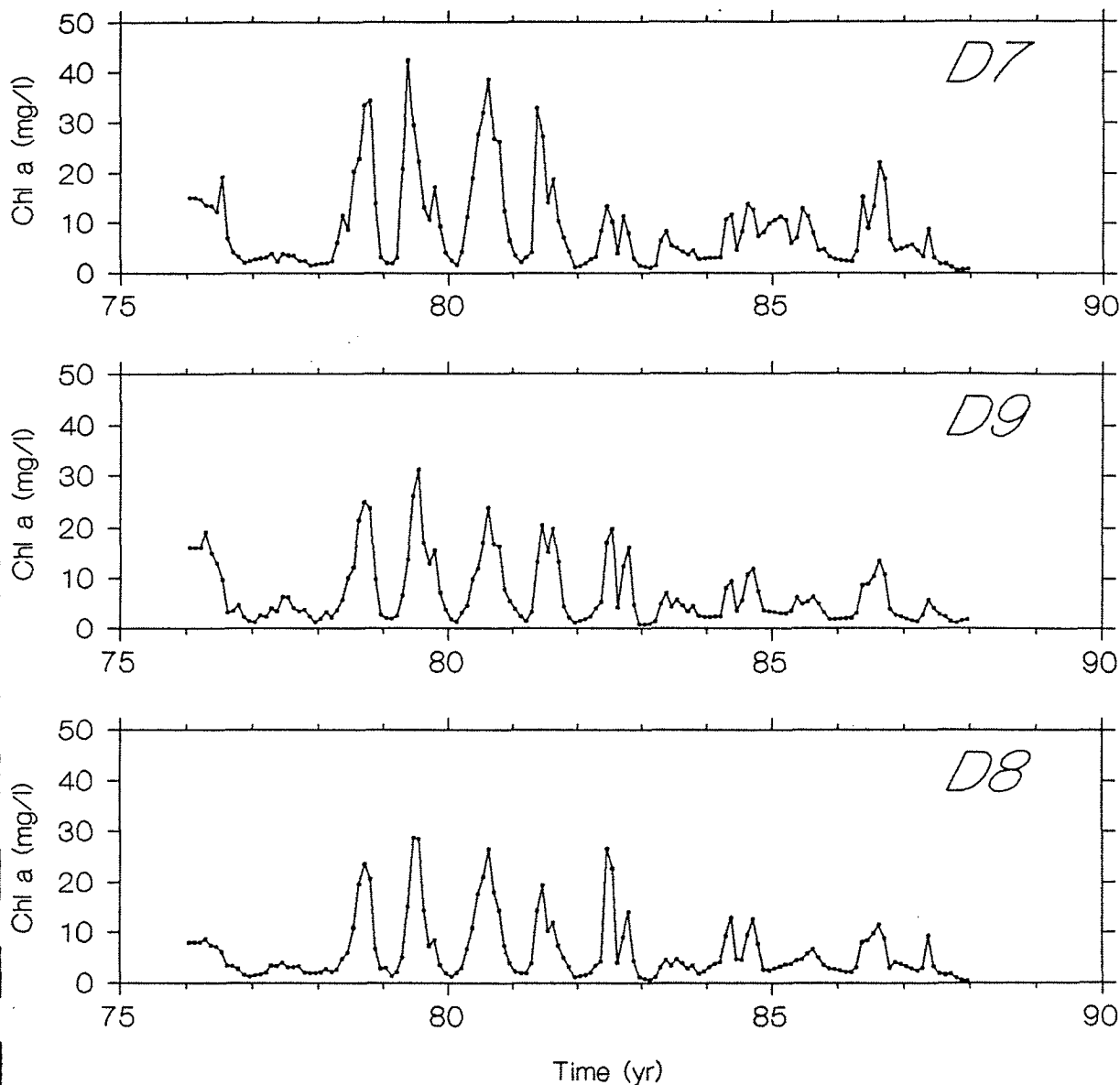


Figure A.10 Monthly mean chlorophyll *a* concentrations in Grizzly (D7) and Honker (D9) bays, and in the channel Suisun Bay (D8; data from DWR).

... (D7) and a Honker Bay (D9) shoal station suggest that phytoplankton productivity in Suisun Bay has been depressed since 1982-1983 (Fig. A.10). Productivity in 1977 also appeared to be low.

As in San Pablo Bay, recent trends for tidal marsh area cannot be evaluated. Point sources, when they were four times higher in 1970 (Fig. A.5), may sometimes have been as significant as phytoplankton or tidal marsh sources, but even then they would have been secondary to loading from Delta discharge.

Mechanisms of interannual variability. Loading of organic carbon from Delta discharge depends both on the volume of discharge and the riverine concentrations of phytoplankton and other forms of labile organic materials. The details of phytoplankton dynamics upstream of Suisun Bay are beyond the scope of this analysis. It should be noted, nonetheless, that several long-term changes in upstream chlorophyll concentration and community composition have occurred since 1973 (see Ball 1987a,b for a detailed analysis). Despite these trends and other types of interannual variability in riverine concentrations upstream, annual chlorophyll loading in recent years appears to be largely proportional to annual Delta discharge (Fig. A.8). Variability in river-borne phytoplankton is evidently inadequate to mask the effects of flow volume.

As pointed out previously, the key to understanding phytoplankton productivity in Suisun Bay is a comprehension of the processes controlling shoal phytoplankton biomass. The same can be said for San Pablo Bay, where three-quarters of the 1980 production took place in the shoals (Table A.3). Two main processes underlying interannual variability have been implicated. The first is the effect of Delta outflow on the residence time for phytoplankton biomass. Much of the work on phytoplankton activity within the northern reach of San Francisco Bay has focused on the significance of the entrapment zone resulting from estuarine circulation (Peterson 1975). Net water column productivity is almost always negative in the channel because of the low Z_p/Z_m ratio, so biomass must be imported for accumulation to take place. During periods of high Delta outflow, an entrapment zone becomes positioned in the channel of San Pablo Bay that increases the residence time of algae dispersed from shoals by tidal mixing and allows such biomass accumulation. As flows decrease, the entrapment zone moves into Suisun Bay where it performs a similar function (Sec A.5.5). During particularly low flows, the entrapment zone is located in the western Delta. A second entrapment zone in the vicinity of the Pinole shoal at lower Delta outflows down to about $300 \text{ m}^3 \text{ s}^{-1}$ has been suggested (Williams and Hollibaugh 1987), but this has been disputed (Ball 1987b). Arthur (1975) first hypothesized that positioning of the entrapment zone relative to large expanses of shoal area was the most critical factor regulating accumulation of phytoplankton in the zone. Further work has largely borne out this contention (Arthur and Ball 1979, 1980; Ball 1977, 1979; Cloern et al. 1983, 1985; Catts et al. 1985; Ball 1987a).

Although the position of the entrapment zone clearly affects the spatial distribution of chlorophyll and POC, the spatial distribution of primary productivity need not reflect that of biomass. When an entrapment zone is present, the residence time for certain phytoplankton taxa and detrital particles is increased and physical transport losses are thus smaller. Perhaps even more important, the concentration of food particles permits more efficient feeding by the planktivores known to frequent the zone. Nonetheless, in the channel, the zone may still be an area of reduced or even negative primary productivity because of a low Z_p/Z_m ratio. If productivity is negative in a region, then biomass accumulation only enhances respiratory losses. For the entrapment zone to stimulate primary productivity, shoal residence time must be effectively increased by its proximity. This is probably, in fact, the case: By decreasing the gradient of biomass between shoal and channel, the entrapment zone probably suppresses net mixing losses of biomass from the shoals. Indeed, the close relationship between shoal and

channel chlorophyll testifies to the effectiveness of tidal mixing between the two regions (Fig. 10).

The relationship between the entrapment zone and shoal biomass (and, presumably, productivity) is not a simple one. Rather than determining a unique biomass, the location of the entrapment zone appears to set bounds on a range of possible biomass levels. This can be most easily appreciated by examining the relationship between chlorophyll and Delta outflow at a shoal station (D7; Fig. A.11). River flow creates an envelope of possible chlorophyll concentrations that narrows at both high and low flows. The maximum of the smoothed scatterplot (LOWESS algorithm; Cleveland 1981) occurs at about $250 \text{ m}^3 \text{ s}^{-1}$, the approximate center of the flow range that positions the entrapment zone in Suisun Bay. But chlorophyll values are quite variable within the envelope and it is clear that positioning of the entrapment zone is not the whole story.

An additional source of interannual variability in biomass appears to be consumption by benthic herbivores. Nichols (1985) detailed how the Atlantic soft-shell clam *Mya arenaria* and other estuarine benthic invertebrates become established in Suisun Bay during drought periods such as 1976-1977. The larvae are carried upstream in the river-induced gravitational circulation and are able to colonize sites in Suisun Bay when salinity increases during dry years. In 1977, the estuarine species achieved densities sufficient to filter the entire water column approximately once per day. Similar appearances of *Mya* in 1962, 1981, and 1985 in Grizzly Bay suggest that about 16 months of consecutive low river inflow were necessary for successful colonization to take place (Nichols 1990). The return of higher inflows eliminates estuarine species, resulting in decreased feeding pressure from the benthic invertebrate community.

This relationship between prolonged low river flow and temporary invasion by estuarine benthic invertebrates may have been upset in 1987 by the appearance of the Asian corbulid clam *Potamocorbula amurensis* (Carlton 1990). The clam was probably introduced from the western Pacific by the release of seawater ballast into San Francisco Bay in the mid-1980s. By 1987, *Potamocorbula* had become numerically dominant at shoal and channel sites in both Suisun and San Pablo bays, and was also present at some South Bay sites. The rapid spread has been attributed to a depauperate benthic community following the flood in early 1986, which resulted in a lack of competition from pre-existing species (Nichols 1990). Low river inflow had again become prolonged for a period of 16 months by 1988, but *Mya arenaria* did not appear in its usual numbers, apparently excluded somehow by the new arrival.

Implications for the near future. Low phytoplankton productivity may persist as long as conditions -- namely low freshwater flows -- favor estuarine benthic macroinvertebrates. Although riverine loading probably will increase once flows are restored, the same cannot be said of phytoplankton productivity. *Potamocorbula amurensis* is able to tolerate an extremely wide range of salinity (at least 1-30 ‰), suggesting that it will not be dislodged by the return of higher river inflows (Nichols 1990). If so, enhanced grazing pressure from benthic invertebrates will continue, depressing local populations of phytoplankton and perhaps benthic microalgae. Lower microalgal productivity could therefore persist for some time.

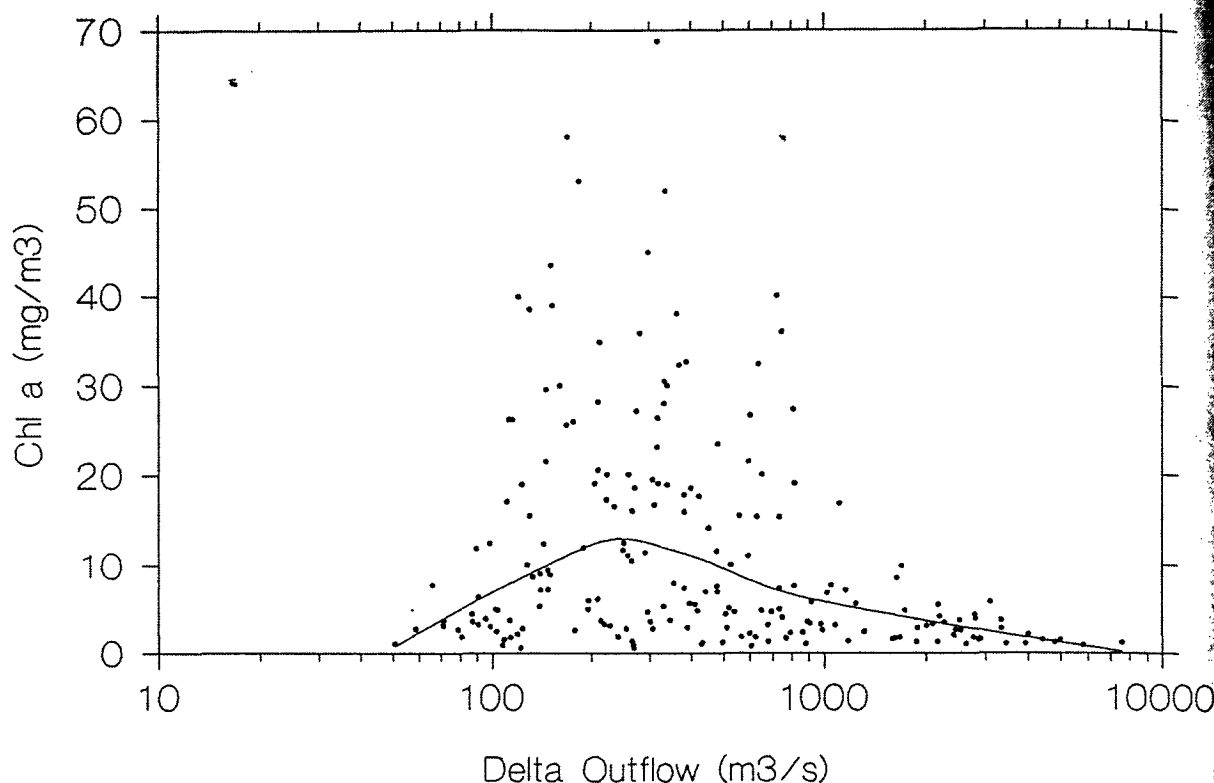


Figure A.11 Monthly mean chlorophyll *a* vs. Delta outflow in Grizzly Bay shoals (D7), Mar 1971-Sept 1988; solid line, LOWESS fit (data from DWR).

As long as Delta discharge is low, organic carbon loading should remain at depressed levels as well. In contrast to microalgal productivity however, riverine organic carbon sources should be restored with the return of higher flows. As a result, the relative importance of organic carbon from riverine loading can only increase. Given the apparent dependence of chlorophyll and perhaps "usable" TOC on annual Delta discharge, the relation between organic carbon sources for the food web and the magnitude of Delta discharge may thus become even more clearcut with the presence of *Potamocorbula*.

The response of marsh export to river discharge is of interest. The magnitude of Delta outflow undoubtedly has some modulating effect on exchange between tidal marsh and open water. The smaller freshwater supply during drought conditions also should favor the spread of estuarine macrophytes in their competition with freshwater macrophytes, changing the habitat areas available for higher organisms. But if the net effects on marsh export are damped compared to the response of organic matter loading and phytoplankton productivity, then marsh export may increase in importance during drought periods. Consider, for example, 1988, when Delta outflow was only 14% of its 1980 value. If "available" TOC loading changed in proportion to Delta outflow, and phytoplankton productivity decreased by a factor of, say, three, then Delta loading and phytoplankton productivity each would have amounted to only $0.02-0.03 \times 10^{11} \text{ g}$.

yr-1. In comparison, if tidal marsh exports were unaffected by outflow, estimated export would still be 0.06×10^{11} (Table A.4). Tidal marsh export consequently may be a more notable source of organic carbon during drought periods.

A.6 FOOD WEB CONSIDERATIONS

A.6.1 Partitioning between food web and outflow

Previously, we mentioned that an explicit assessment of organic carbon sinks would not be undertaken. Certain aspects of these sinks must be addressed, however, if we are to properly understand the implications of the sources and their respective magnitudes. New organic carbon resulting from either autochthonous production or allochthonous contributions has essentially two possible fates: It can enter the food web through various means, or it can be exported from the region without being utilized. This mass balance can be expressed ideally as

$$\Sigma J_i = (C/T_c) + (C/T_h),$$

where J_i ($\text{g m}^{-3} \text{d}^{-1}$) is the i th carbon source; C (g m^{-3}) is the concentration of unutilized organic carbon within the subembayment; T_c (d) is a "primary consumption" residence time, that is, the time that would be required for all primary consumers to strip the subembayment of new organic carbon, either through assimilation by bacteria, zooplankton, or benthic invertebrates; and T_h (d) is a "hydraulic" residence time for new organic carbon due to flushing. Note that T_h is actually different for DOC and various kinds of POC, due to the possible presence of an entrapment zone, but this complication will not obscure the basic point to be made here. The fraction of organic carbon sources entering the food web is thus

$$f_c = (C/T_c) / [(C/T_c) + (C/T_h)],$$

which reduces to

$$f_c = 1 / [1 + (T_c/T_h)].$$

The fraction entering the food web at any time accordingly decreases in a simple fashion with the ratio of primary consumption to hydraulic residence times.

Residence times -- and their ratio -- have a marked seasonality. In 1980, for example, monthly mean Delta discharge during January was about $3000 \text{ m}^3 \text{ s}^{-1}$. Hydraulic residence times in Suisun Bay at these flows are on the order of 1 d (Smith 1987). On the other hand, monthly mean Delta discharge in August was $110 \text{ m}^3 \text{ s}^{-1}$. The corresponding hydraulic residence time is on the order of 10 d (Smith 1987). For purposes of illustration, consider a benthic invertebrate community that filters the overlying water at a rate of 0.2 d^{-1} , constant throughout the year; T_c is thus 5 d. During January, the corresponding f_c in Suisun Bay would be less than 20%, during August, almost 70%. Typically, however, benthic invertebrate populations attain their highest abundance -- and, presumably, lowest T_c -- between spring and fall (Nichols and Thompson 1985b). T_h and T_c therefore tend to be out of phase, implying even a larger seasonality in f_c .

This seasonality in f_c forces us to confront a fundamental deficiency with assessing organic carbon sources on an annual basis: The individual organic carbon sources also change radically with the seasons. In 1980, for example, 35% of DOC imports from the Delta occurred in January, less than 5% in August. Suisun Bay primary productivity, in contrast, peaked in August and was negligible in January. The actual contribution of an individual source to the food web thus depends on the temporal matching of its flux J and f_c . More formally, although the annual contribution of the i th carbon source to the organic carbon pool is simply the time integral of J_i , the annual contribution to the food web is the time integral of $J_i \cdot f_c$. Because high river flow decreases T_h but apparently increases J_i due to riverine loading (Fig. A.8), there is an inherent mismatch between riverine sources and f_c (although the presence of an entrapment zone at $100\text{--}300\text{ m}^3\text{ s}^{-1}$ [Ball 1987a] would increase T_h and f_c over the values expected on the basis of flow volume alone). Furthermore, because of the inhibitory effect of river flow on consumer populations, the mismatch could be exacerbated by an increase in T_c during high flow. In contrast, seasonality favors the contribution of primary productivity sources to the food web. A higher proportion of organic carbon derived from primary productivity than from riverine sources is probably consumed on an annual basis. These considerations constitute a strong argument for taking the next step in assessing organic carbon sources, namely, aiming for a higher resolution in time.

Although a large proportion of organic carbon sources for Suisun Bay may never enter the food web of the subembayment, particularly in winter, the same cannot be said for the northern reach as a whole. When we consider the quantity f_c for the entire northern reach of the estuary, a much higher fraction probably enters the food web. The northern reach has hydraulic residence times three-fold higher than for Suisun Bay alone (Walters et al. 1985). Furthermore, benthic invertebrate biomass may be substantially higher -- and T_c lower -- in San Pablo compared to Suisun Bay (Thompson and Nichols 1981). Thus, much of the organic matter for Suisun Bay attributed to Delta discharge may actually be consumed within San Pablo Bay.

Assuming that available riverine TOC is 10% of the total riverine loading (Sec. A.3.1), the combined contribution of all organic carbon sources is $1.1 \times 10^{11}\text{ g C yr}^{-1}$ for the northern reach (including Suisun, San Pablo, and half of Central Bay sources). For this northern reach as a whole, phytoplankton productivity is the only major source (50%), while benthic microalgal productivity, Delta discharge, and tidal marsh export may be significant secondary sources (10-20% each). A mean $\text{C}:\text{O}_2$ molar ratio for benthic respiration in San Francisco Bay appears to be about 1 (Hammond et al. 1985). If respired within the estuary, the carbon sources could thus give rise to an oxygen consumption of $2.9 \times 10^{11}\text{ g yr}^{-1}$. In comparison, Peterson (1979) estimated a substrate oxygen consumption of $2.3 \times 10^{11}\text{ g yr}^{-1}$ for the northern reach, about 20% less than our estimate. Peterson's assessment was based on a mass balance for oxygen using primary productivity and respiration measurements for 1976-1977, estimates of transport across the air-water interface, and an assumption that net dispersive transport of oxygen was zero in the horizontal direction. Production in 1976-1977 was probably lower than in 1980 and secondary carbon sources were ignored, so the method used by Peterson (1979) should yield a higher estimate for 1980. The agreement between the estimates made on the basis of organic carbon sources and by Peterson (1979) is remarkable, and perhaps fortuitous in view

of the many approximations and uncertainties involved. Nonetheless, the agreement offers some support for both estimates and implies that most organic carbon sources for the northern reach enter the food web within the reach.

Similar evidence suggests that most South Bay organic carbon sources are consumed within South Bay. Hydraulic residence times for South Bay are much higher than for the northern embayments; T_h is probably on the order of 10^2 d, even during high river flow. Benthic biomass is probably higher, and T_c lower, than for either San Pablo or Suisun bays (Thompson and Nichols 1981). Finally, benthic gas exchange measurements suggest that most of the primary productivity is consumed within South Bay. Hammond et al. (1985) estimated an annual average of 23 ± 6 (SE) $\text{mmol m}^{-2} \text{d}^{-1} \Sigma \text{CO}_2$ in 1980, based on quarterly, in situ measurements of benthic flux at both a shoal and channel site. The June 1980 measurement was close to the only previous estimate of benthic flux -- for August 1976 (Hammond and Fuller 1979). The daily average for 1980 is equivalent to an annual consumption of $0.55 \times 10^{11} \text{ g C yr}^{-1}$ for South Bay. In comparison, the organic carbon sources in South Bay for 1980 totalled $1.2 \times 10^{11} \text{ g C yr}^{-1}$. About half of the estimated production thus appears to be metabolized on the bottom. Additional respiratory losses must take place in the water column through bacterial and zooplankton metabolism. Although oxygen consumption measurements have been published for the water column of the northern reach (Peterson 1979, 1987, 1988), no annual averages have been estimated for South Bay. In any case, the data imply that at least half of the organic carbon sources for South Bay enter the food web within the subembayment.

The high proportion of organic carbon sources apparently consumed within the estuary underlines an important point: Organic material which is unavailable to one population because of size, shape, composition, or precise location may have many other opportunities to enter the food web. For example, the alga *Melosira granulata*, common in Suisun Bay and especially parts of the Delta (Herrgesell 1990), is not a particularly good food source for zooplankton because of its hard siliceous frustule. On the other hand, these *Melosira* filaments undoubtedly die within the estuary and become incorporated into the food web through bacterial decomposition or perhaps direct consumption by benthic invertebrates.

Physical transport remains a possible complicating factor in interpretation of the oxygen data. For example, it is possible -- at least logically -- that physical transport results in both significant organic carbon sources and biomass losses. If the two approximately balance, then primary productivity and community respiration could appear to balance as well; it would be erroneous in that case, however, to conclude that respiration was the only significant fate for primary productivity. In fact, for estuaries as a group, annual benthic respiration accounts for an average of only about 25% of organic carbon sources (Nixon 1981b), substantially less than what the data appear to imply for San Francisco Bay.

A-6.2 Organic carbon sources and higher organisms

The effect of food supply on aquatic resources of the Bay can be broken down into three successive issues: (1) the supply of new organic carbon by primary productivity and imports; (2) the partitioning of this new organic carbon between an unutilized outflow and entry into the food web; (3) and the flow of organic carbon from new organic carbon entering the food web to the populations of interest, whether they be fish, shellfish, and so on. Previous sections have dealt with the first two issues -- particularly the first -- in some detail. The last issue is the most complex one, and certainly the least understood. It is not possible to be as systematic about organic carbon flow *within* the food web as we have tried to be about organic carbon sources *to* the food web. One particular finding based on studies of many estuaries, however, is worthwhile reviewing here.

Despite our lack of knowledge regarding the particulars of food webs, certain simplifications have emerged regarding fish production from a synthesis of work in many different aquatic ecosystems. In particular, whether in marine or freshwater systems, fish yield tends to increase with annual primary productivity and, presumably, other organic carbon sources (e.g., Nixon 1988). For marine (including estuarine) systems, fish yield is proportional to the 1.6th power of primary productivity ($R^2 = 0.84$, $p < 0.05$), suggesting that primary productivity changes are amplified in fish yield changes. The slope of the relationship may be even higher for estuaries (Nixon 1988, Fig. 6). Given that organic carbon sources for certain embayments such as Suisun Bay (Sec. A.5.4) have decreased during the recent drought period, it is tempting, on the basis of this empirical relationship, to conclude that the overall yield of fish and macroinvertebrates must have decreased as well. Although this may very well be true, a number of caveats are in order.

First, even if this rule-of-thumb connecting fish yield and primary productivity does reflect the effects of food supply, it would be unwise to assume too great a precision. The relationship was established with productivity data ranging over a factor of 20. Over the much smaller range probably characteristic of San Francisco Bay during the last decade, the variance explained by this relationship is much less and other factors are correspondingly more significant.

Second, a more recent analysis of total fish yield in coastal and open ocean waters concluded that carnivorous fish production is controlled by the amount of "new" nitrogen (as opposed to recycled nitrogen) annually incorporated into phytoplankton biomass (Iverson 1990). The relationship between fish yield and total primary production (Nixon 1988) is therefore just a surrogate for the true causal relationship between fish yield and "new" primary production. Little evidence exists that San Francisco Bay -- as opposed to the Delta -- is nitrogen-limited, so it is unclear how well this relationship can be applied to the Bay.

Finally, the relationship addresses only overall fish yield. Although overall yield may increase -- a conclusion which cannot be verified for the Bay because of insufficient data -- the same cannot be said for individual species of interest. Each population will react according to its habitat and food requirements, undoubtedly resulting in a shift in species composition.

Drought conditions in San Francisco Bay, for example, not only depress autochthonous and allochthonous energy sources, but also result in relatively more grazing losses to benthic macroinvertebrates (Sec. A.5.4). Benthic food webs are therefore favored, and a greater *proportion* -- not necessarily a greater amount because of the reduced organic carbon supply -- can pass to demersal fish such as sturgeon (*Acipenser transmontanus*; Nichols 1990). If *Potamocorbula amurensis* persists even after drought conditions cease, the increase in relative importance of benthic pathways may also persist.

A.7 DATA AND INFORMATION GAPS

Phytoplankton productivity. Changes in the array of sampling stations are warranted. Two issues in particular need to be addressed. First, primary productivity in shoal areas dominates that in deeper areas, especially in Suisun Bay (Table A.3), yet most data are collected from channel stations. Second, almost no long-term series of chlorophyll or productivity measurements are available for Central and San Pablo bays. Little is known, consequently, about the entrainment zone when it is pushed out of Suisun Bay by high flows. Third, certain areas in South and Suisun bays appear to be oversampled in space, relatively speaking. In the South Bay, for example, the region between San Bruno shoal and the Dumbarton Bridge exhibits much less spatial variability than the region between the Golden Gate Bridge and San Bruno shoal (Fig. A.6). A similar analysis of data landward of the Carquinez Strait reveals tight clusters of stations, such as from Chipps Island to Point Sacramento.

Time series for the Bay are thus characterized by periods with relatively high frequency data, and regions with relatively high-resolution data, interspersed with long gaps in time and space. The irregularity in sampling hinders the potential value of the data that are collected, particularly for understanding the long-term changes that may now be underway globally. A commitment needs to be made to a group of "index stations" that will be sampled at a regular frequency for at least chlorophyll *a* and extinction coefficient (or, equivalently, photic depth) into the indefinite future. Some of the current effort in the channels should be shifted to shoal sites. Similarly, some of the current efforts in South and Suisun bays should be shifted to Central and San Pablo bays. If this basic, "index station" program is made as simple as possible, its longevity would be more likely. The number of stations and the sampling frequency should therefore be as modest as possible. The abundance and distribution of benthic organisms should be carefully considered in choosing index stations, as the benthos provide a kind of "integrated moving-average" indication of chemical and planktonic conditions.

Actual primary productivity measurements are not necessary, as productivity can be deduced from biomass, turbidity, and light availability (Sec. A.2.1). But given the importance of light availability, a permanent station should be established for measuring surface irradiance. The absence of continuous, reliable, irradiance measurements hinders the interpretation of existing data sets.

Assumptions about aphotic respiration have a large effect on estimated productivity, particularly in Suisun Bay (Table A.3). Yet little direct evidence exists on the magnitude of these respiratory losses. Further experimental work on aphotic respiration in San Francisco Bay would be a definite contribution, particularly work that would improve estimates of net water column productivity P_{nw} .

Benthic microalgal productivity. No measurements have yet been made on benthic microalgal productivity, despite their possible significance, especially in South and Central bays (Table A.4). As discussed previously (Sec. A.2.3), prevailing measurement techniques may be

unreliable. Although suitable methods may not be available for San Francisco Bay, this issue does require more attention. At the very least, sampling of sediment chlorophyll could accompany water column measurements at index stations. The product of sediment chlorophyll and light incident on the sediments could serve as a relative index of benthic productivity. Incident light could be estimated from measurements of surface irradiance and extinction coefficient (photic depth) at the sampling stations.

Delta discharge. Delta discharge may be the largest source of organic matter for Suisun Bay and is probably a significant one for the northern reach as a whole (Table A.4). The load of organic carbon to San Francisco Bay from the Delta needs to be measured on a regular basis. Due attention needs to be given to POC as well as DOC, and to bottom samples as well as near-surface samples. Because of the probable episodic nature of organic carbon loading, sampling must be able to resolve the succession of storms that characterize the winter period. Because of the apparent importance of riverine algae, chlorophyll and derived pigments also should be measured in tandem with organic carbon.

The issue of availability needs to be addressed as well. BOD measurement offers one perspective on this problem. Ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.) need to be continued and extended. Additional approaches also must be sought.

Tidal marsh export. Tidal marsh sources may be of importance for Suisun Bay, particularly during drought periods. Direct estimates of tidal marsh export are virtually impossible, in part because of the difficulty in determining residual flows from tidal exchange. The uncertain availability of exported organic carbon is another obstacle. Hence, indirect methods are required to address this question. The use of multiple stable isotope markers appears to be of value. B.J. Peterson et al. (1985), for example, using ^{13}C , ^{15}N , and ^{34}S , was able to show that benthic macroinvertebrates consumed *Spartina* detritus and plankton in preference to terrestrial plant detritus. A similar study in Suisun Bay may be able to determine at least the qualitative significance of tidal marsh export.

In view of the large export of reduced sulfur encountered for some marshes (Sec. A.3.2; Peterson et al. 1980), a preliminary investigation of sulfide oxidation activity related to tidal marsh exports is warranted.

Circulation and mixing. The system boundaries need to be considered carefully in relation to physical transport. At the minimum, transport through the Golden Gate requires definition and should be the first objective. A carbon budget for the entire Bay would then be feasible.

Further subdivision needs to be done carefully, with due regard to topographical features and the existing data. As implied in the previous discussion (Sec. A.5.3), the segmentation scheme normally used landward of the Golden Gate requires some revision. The boundary between South and Central bays, in particular, perhaps should be shifted to the San Bruno shoal. The northern extent of "Central Bay", currently at Point San Pedro-Point San Pablo, also

requires re-examination from a hydrodynamic point of view. In addition, the utility of the boundary between San Pablo and Suisun bays needs to be addressed. The entrapment zone, as well as organic matter from riverine loading, moves freely across the boundary as flows increase. From the point of view of establishing subregions for a carbon budget and subsequent food web analysis, the distinction between the two subembayments may have little value. On the other hand, a further subdivision of South Bay at the Dumbarton Bridge appears warranted, in view of the higher point source loading, relative tidal marsh area, and runoff south of the bridge. A lack of primary productivity measurements in lower South Bay would be an impediment to this subdivision, something to be considered also in the choice of index stations (see above).

Whatever the boundaries, direct measurements of transport are an unrealistic goal, for the same reason that tidal marsh export cannot be assessed with any accuracy. But the flow field can be characterized from existing data and modeling studies. In principle, the flow data can be combined with concentration data for various organic matter fractions to estimate transport across the major boundaries. In practice, the concentration data does not appear to be adequate in many locations. Modelling studies, therefore, must be accompanied by a supplemental field measurement program for organic matter fractions, particularly DOC, various size fractions of POC, and chlorophyll. At the minimum, measurements are needed at the Golden Gate, including horizontal gradients through the Gate and vertical profiles both seaward and landward of the Gate.

Food web structure. The structure of the food web connecting organic carbon sources to higher organisms is critical in determining the magnitude of their food supply. The number of trophic linkages, for example, is especially important in controlling the efficiency of energy transfer from sources to macroscopic consumers: If energy is transferred with an average efficiency of, say, 10% along each link, then the interposition of an intermediary organism has the same effect as a ten-fold drop in the food supply at the base of the food web.

At the macroscopic level, food webs have been delineated in a number of ecosystems, as recently reviewed by Schoener (1989). At the microscopic level, on the other hand, the relative importance of many postulated pathways has not yet been demonstrated (Mann 1988), for the Bay or for other ecosystems. In view of the nature and number of these microscopic interactions -- involving autotrophs, DOC, bacteria, protozoans and small metazoans -- a complete characterization of the Bay's food web appears to be an unrealistic goal for the near future.

It is possible, nevertheless, that a complete characterization is unnecessary. Circumstantial evidence from other ecosystems suggests that the major pathways through the food web are sometimes relatively simple. Demersal fish production, for example, often has a high efficiency when compared to organic carbon sources for the benthos (reviewed by Mann 1982). Energetic considerations require that settling organic matter be consumed directly by macrofauna and passed to demersal fish in order to account for this high efficiency. If the other components of the benthos do, indeed, have a secondary role, then the current lack of quantitative knowledge regarding bacteria, microfauna, and meiofauna in San Francisco Bay sediments (Nichols and Pamatmat 1988) may not be a major impediment. Note, however, that the "small food web"

consisting of micro- and meiofauna does compete for food with the macrobenthos of some estuaries (e.g., Wadden Sea; Kuipers et al. 1981).

A comparison of benthic macroinvertebrate productivity (e.g., Nichols 1978) with primary productivity would be especially pertinent, particularly during bloom periods when most of the annual phytoplankton production takes place. If macroinvertebrate productivity were a high enough percentage of microalgal productivity, then a direct link from primary producers to the large benthic invertebrates would be implicated. Lower percentages would imply either that intermediate consumers were present in the water column or sediments, or that the planktonic food web was a significant sink for organic matter. A related study in the South Bay is currently in the initial planning stages (J. Thompson 1990, pers. comm.). A similar investigation is warranted for Suisun Bay. The results of these studies, combined with ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.), should provide a guide for further research within the benthic habitat.

Even though the major pathway *within* the benthic habitat may be simple, organic matter from primary productivity may undergo transformations *before* coming into contact with the benthos. The number of trophic links in the water column may radically affect the food supply to midwater fish and the benthic habitat, whether these links occur on a microscopic -- via the "microbial loop" (Azam et al. 1983) -- or macroscopic level. Indeed, bacterioplankton production and grazing by planktonic bacteriovores appear sometimes to form a significant pathway in the Bay's food web (Hollibaugh and Wong, pers. comm. 1991). A continued investigation into planktonic microbial processes is therefore warranted. The detailed study of mechanism, however, should be accompanied by attempts to determine whether a few simple pathways dominate. As in the case of the benthos, simultaneous measurement of both organic matter sources and production of the larger planktonic invertebrates may provide the necessary clarification. These measurements would be most informative if done in conjunction with those for the benthos.

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Appendix B

Distribution of commonly occurring fish species in San Francisco Bay

Each area within the Bay supports a distinctive association of fish species. The following tables describe the six most regularly captured species in each of the four seasons at each of the sampling sites of the CDFG Bay Study. The criterion by which species were included at a station was that the species must have been caught in at least one-third of the trawls made at the station in the one season. This criterion led to inclusion of three categories of species:

1. species which were always abundant in appropriate season and were caught in most trawls, for instance northern anchovy.
2. species which were rare but regular so that they were captured occasionally throughout the ten years of the study, for instance white sturgeon.
3. species that were very abundant during at least one-third of the years of the study, for instance longfin smelt were captured in almost every trawl in San Pablo and Suisun Bay during the first three years of the study but by 1992 were extremely rare.

In sum, these are the species that characterize each station but they cannot be expected in all years.

Species abbreviations used in the following tables are:

AMS	American shad	<i>Alosa sapidissima</i>
BAT	California bat ray	<i>Myliobatis californicus</i>
BAY	bay goby	<i>Lepidogobius lepidus</i>
BRN SMO	brown smoothhound	<i>Mustelus henlei</i>
BROK	brown rockfish	<i>Sebastes auriculatus</i>
CCAT	channel catfish	<i>Ameiurus punctatus</i>
DAB	speckled sanddab	<i>Citharichthys stigmaeus</i>
DS	Delta smelt	<i>Hypomesus transpacificus</i>
ENGL	English sole	<i>Parophrys vetulus</i>
JACK	jacksmelt	<i>Atherinopsis californiensis</i>
KS	chinook (king) salmon	<i>Oncorhynchus tshawytscha</i>
LEOP	leopard shark	<i>Triakis semifasciata</i>
LFS	longfin smelt	<i>Spirinchus thaleichthys</i>
LOGP	bigscale logperch	<i>Percina macrolepidotus</i>
MID	plainfin midshipman	<i>Porichthys notatus</i>
NAC	northern anchovy	<i>Engraulis mordax</i>
PH	Pacific herring	<i>Clupea harengus</i>
SB	striped bass	<i>Morone saxatilis</i>
SF	starry flounder	<i>Platichthys stellatus</i>
SP	shiner perch	<i>Cymatogaster aggregata</i>
ST	Sacramento splittail	<i>Pogonichthys macrolepidotus</i>
STAG	staghorn sculpin	<i>Leptocottus armatus</i>
TFS	threadfin shad	<i>Dorosoma petenense</i>
TOP	topsmelt	<i>Atherinops affinis</i>
WALL	walleye surfperch	<i>Hyperprosopon argenteum</i>
WCAT	white catfish	<i>Ictalurus catus</i>
WCRK	white croaker	<i>Genyonemus lineatus</i>
WS	white sturgeon	<i>Acipenser transmontanus</i>
YFG	yellowfin goby	<i>Acanthogobius flavimanus</i>

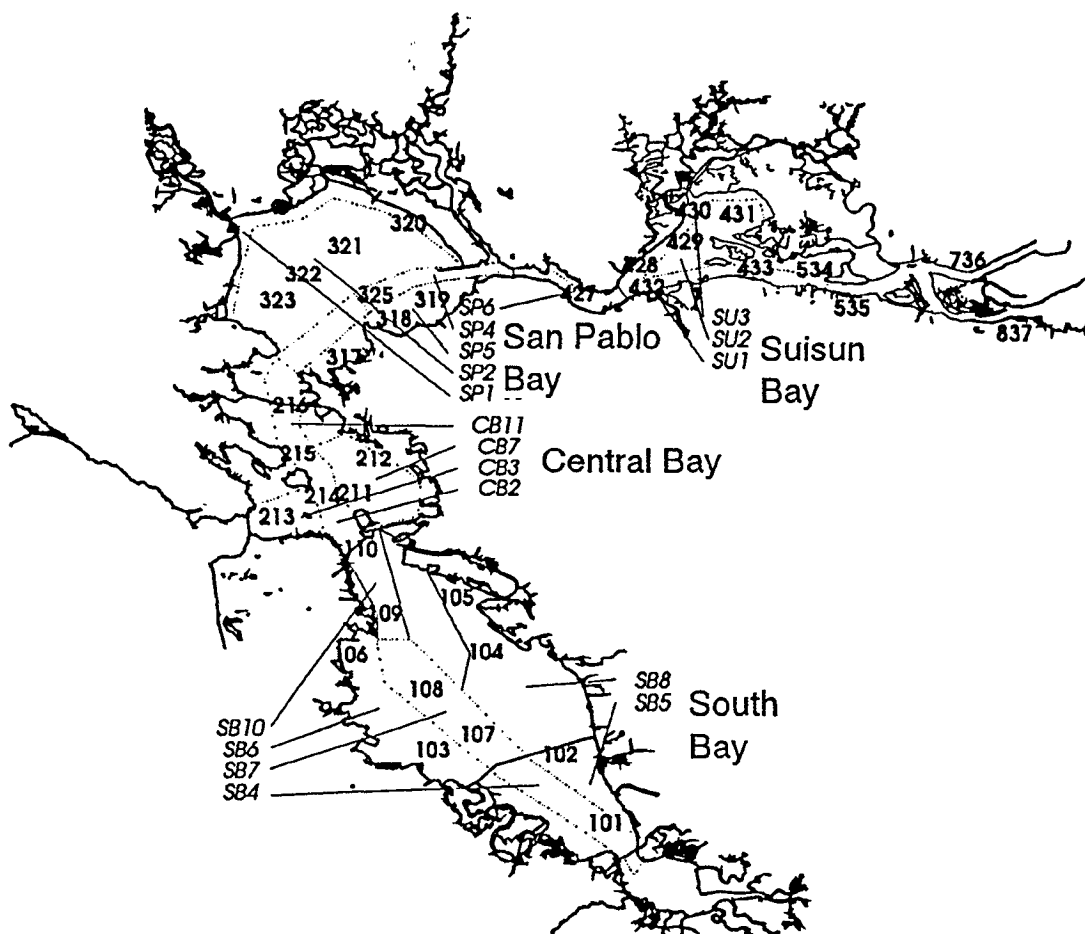


Figure 97 Sampling sites (in bold) of the CDF&G Bay Study and corresponding segments of the Bay

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	LFS	SP	PH	TOP		19	798 3665
Apr-Jun	NAC	JACK	SP	PH	LFS		20	878 10639
Jul-Sep	NAC	BAT	JACK	MID			12	345 9823
Oct-Dec	NAC	TOP					14	255 2821

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	SP	STAG	BAY	ENGL	LFS	34	1785 2652
Apr-Jun	NAC	WCRK	SP	BAY	STAG	BRN SMO	22	758 991
Jul-Sep	NAC	WCRK	MID	BRN SMO			24	424 1157
Oct-Dec	NAC	SP					21	212 366

Northern anchovy is the most frequently captured species in both nets. Several fish species increase in abundance during the season when anchovy abundance is low but their small increases are masked, when considering the total catch figures, by the large drop in catch of anchovy.

Pacific herring and shiner perch are regular components in the midwater trawl from January to June. Jacksmelt are regularly caught from April to September in the midwater trawl. Topsmelt and longfin smelt are caught regularly during parts of the rainy season; topsmelt principally from October to March and longfin smelt from January to June. Bat rays and plainfin midshipmen regularly enter the trawls in summer.

In the otter trawl there is a peak in numbers of species and numbers of fish from January to March. White croaker and brown smoothhounds are regularly caught in the warmer months (April - September). In the cooler months, shiner perch are regularly caught from October to June and bay gobies are caught from January to June.

In both nets there is a peak in number of species and in the number of predictable species from January to June and the least predictability from October to December.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	NAC	LFS				16	1239 3189
Apr-Jun	NAC	PH	JACK	SP			17	623 16733
Jul-Sep	NAC	JACK					13	677 8695
Oct-Dec	NAC	TOP	JACK				15	215 4476

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	NAC	STAG	DAB	BAY	LFS	32	1293 1455
Apr-Jun	WCRK	NAC	SP	BAY	STAG	ENGL	22	738 935
Jul-Sep	NAC	WCRK	SP	BAY	MID		18	486 631
Oct-Dec	NAC	WCRK					19	287 317

As with station 101, northern anchovy is a regular feature of the catch in all seasons in both nets at station 107 and the season of greatest abundance of the other species is January to March when anchovy are least abundant.

The midwater complement of species regularly caught at this station is smaller, principally Pacific herring from January to June with jacksmelt characterizing the catch from April to December.

In the otter trawl shiner perch and bay goby are predictable elements of the catch for three seasons from January to September. White croaker are very consistently present from April to December, and only slightly less so in the remaining months. Plainfin midshipmen, as at station 101, are regularly present in the summer.

In the otter trawl the same pattern is found as at station 101, of greater species diversity from January to March and higher predictability from January to June. On the other hand the species richness in the midwater trawl stays low throughout the year.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						18	177 218
Apr-Jun	NAC	PH	JACK	SP			14	1921 19999
Jul-Sep	NAC	JACK	PH				11	365 4271
Oct-Dec	NAC						18	221 1462

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	NAC	DAB				25	663 807
Apr-Jun	NAC	SP	BAY	DAB			23	472 967
Jul-Sep							16	207 813
Oct-Dec	NAC						17	119 172

Although located in the same segment as station 107, station 108 displays a very different pattern of species occurrence. Northern anchovy are not predictably present in all seasons, in fact the July to September catch of the otter trawl contains no species more than eight times. The most regularly caught species in the otter trawl at that season is the plainfin midshipman.

In the midwater trawl, northern anchovy regularly dominate the catch from April to December but in the period from January to March only jacksmelt were caught at least a third of the time. Pacific herring are found with greater regularity from April through September, in contrast to their earlier regular occurrence in the more southern stations.

Compared to the other stations in this channel, the otter trawl at station 108 is remarkably bare of regularly occurring species. Fish catch is similar to other stations and winter and spring show an increased number of species, but there are few that occur regularly. The commonly caught species are the two most frequently caught fish in South Bay, northern anchovy and shiner perch.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	PH	LFS				12	207 605
Apr-Jun	NAC	PH	SP	JACK			17	2118 17996
Jul-Sep	NAC	PH					14	2166 18745
Oct-Dec	NAC	PH					14	1631 5772

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	BROK	NAC	WCRK	BRN SMO	LEOP	30	1096 1173
Apr-Jun	WCRK	BROK	BAY	MID	BRN SMO	NAC	27	505 580
Jul-Sep	NAC	BROK	SP	BAY	WCRK	MID	23	601 661
Oct-Dec	BROK	NAC	MID	WCRK			23	467 492

Station 109, in segment SB10, continues the trend of decreasing predictability of the fish fauna as one moves north from station 101. Northern anchovy and Pacific herring are the most abundant and consistent members of the midwater community and even in Oct-Mar, when at low catches, anchovy accounts for 66% and 85% of the midwater catch for the two quarters.

The otter trawl catch is strikingly different than the midwater catch. Species richness is high and many of the species are quite predictable. In addition northern anchovy makes up a very small part of the catch. This difference between the yield from each net probably reflects the greater depth of station 109 than any other channel station in South Bay, and so less overlap in the proportion of the water column sampled by the two nets.

White croaker and brown rockfish, are regularly caught at these stations in all seasons of the year. The occurrence of brown smoothhounds and plainfin midshipmen is earlier than at more southern stations, indicating the movement of these species from the ocean and down the channel. Underlining the greater proximity of this station to the ocean is the regular occurrence of leopard sharks.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	NAC	WCRK	LFS			14	946 1719
Apr-Jun	PH	NAC	WCRK	SP			23	3983 31890
Jul-Sep	NAC	PH	JACK	SP			17	2247 21278
Oct-Dec	NAC	PH					15	374 18911

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	WCRK	NAC	STAG	ENGL	LFS	26	967 1059
Apr-Jun	WCRK	NAC	BAY	MID	ENGL	BRN SMO	26	596 689
Jul-Sep	WCRK	BAY	SP	MID	ENGL	STAG	26	1861 1920
Oct-Dec	WCRK	SP	BAY	NAC	LFS		19	1087 1177

Tremendous abundance of northern anchovy in the midwater trawl is the dominant feature at station 110. Like the other station in SB10, station 110 generally yields most often Pacific herring and northern anchovy, but white croaker are also regular features of the catch from January to June and shiner perch often occur from April to September. Like the other station in this segment, species abundance peaks from April to June with low numbers of species from January to March when more southerly stations show their greatest species diversity.

The otter trawl catches a high diversity of species for most of the year and, many of them are quite regular and seasonal in their presence. White croaker and shiner perch dominate the catch year-round. (shiner perch are not included in the six most frequent species during spring in the table above but they were caught in more than a third of the trawls performed). They are joined regularly by English sole from January to March and by bay goby from April to December. As with station 109, plainfin midshipmen and brown smoothhounds occur earlier here than they do at stations further south.

East side stations
 Segment SB5
 Bay Study Station 102

Midwater Trawl
 Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						8	114 312
Apr-Jun	JACK	NAC	PH	SP			14	495 2659
Jul-Sep	NAC	JACK					10	413 11844
Oct-Dec	NAC	JACK	TOP				8	639 1960

Otter Trawl
 Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL					26	375 426
Apr-Jun	SP	NAC	ENGL	BAY	STAG	WCRK	27	1562 1823
Jul-Sep	NAC	SP					27	278 965
Oct-Dec	NAC	SP					15	172 412

Station 102 in segment SB5 is the southernmost shallow station in South Bay. Northern anchovy is a regular feature of the catch from both nets, but is much more dominant numerically in the midwater net. In the midwater net jacksmelt are a regular feature with anchovy from April to December, while in the otter trawl, during the same months, shiner perch are captured with anchovies.

Species richness is low in the midwater trawl but high in the otter trawl for all of the year except from October to December.

Species predictability in the otter trawl catch is low for most seasons except spring, when 8 of the 27 species collected occur there in more than one third of the trawls made. The cheekspot goby is among those fish characterizing this station.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						8	94 211
Apr-Jun	NAC	JACK	SP	PH	WALL		22	549 1851
Jul-Sep	NAC	JACK	TOP				11	1974 12113
Oct-Dec	NAC						10	146 537

Otter trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL					25	325 442
Apr-Jun	NAC	SP	ENGL	BAY	STAG	PH	30	1116 1448
Jul-Sep	NAC	SP					24	349 918
Oct-Dec	NAC						14	142 459

Northern anchovy and jacksmelt are the most frequently caught fish in the midwater trawl and northern anchovy also dominate the otter trawl catch.

The midwater catch is characterized by the absence of any regularly caught species except anchovy from October to March. The walleye surfperch, which is not caught regularly at any other station on the eastern shore, is a regular inhabitant of this station during the period from April to June.

The otter trawl, as with station 102, dose not yield a very consistent catch except during the spring.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						17	115 228
Apr-Jun	NAC	JACK	PH				13	1473 2598
Jul-Sep	NAC	JACK	PH				13	386 6764
Oct-Dec	NAC	JACK					10	502 1297

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL	DAB					29	260 298
Apr-Jun	SP	NAC	ENGL	DAB	STAG		29	968 1616
Jul-Sep	SP	NAC					21	417 703
Oct-Dec							18	73 504

The second station in segment SB8 is similar to the first; most of the predictability of catch is based on the more ubiquitous species of the South Bay. The midwater trawl results show that northern anchovy, Pacific herring and shiner perch are the only consistent catches throughout the year with the midwater trawl. Again, the otter trawl shows one period of lower species richness in October-December, and one period of high predictability in the spring.

West side stations
Segment SB 6
Station 103

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						9	117 197
Apr-Jun	NAC	JACK	PH	SP			15	1308 12953
Jul-Sep	NAC	JACK	TOP				9	289 12124
Oct-Dec	NAC	TOP	JACK				13	263 850

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL						29	307 328
Apr-Jun	SP	ENGL	STAG	BAY	NAC	DAB	26	1976 2654
Jul-Sep	SP	NAC					23	565 1427
Oct-Dec	SP						26	254 491

The wide shoals on the west side of South Bay are sampled at two stations. Station 103 is at the south end of the shoals. The regular midwater catch includes northern anchovy in all seasons except from January to March, but is remarkable for the year-round presence of jacksmelt. The most consistent catch in the otter trawl is shiner perch except for January to February when English sole is the only one of 29 species to be collected more than eight times in the 27 trawls performed.

As on the east side, only the spring months from April to June display much consistency of catch.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar							14	93 119
Apr-Jun	PH	NAC	JACK	WALL			21	6593 12197
Jul-Sep	NAC	SP	JACK	WALL	PH		16	1467 11143
Oct-Dec	NAC	JACK					12	609 2917

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL					26	349 387
Apr-Jun	BAY	SP	ENGL	WALL	NAC	WCRK	26	2918 2990
Jul-Sep	SP	BAY	NAC	ENGL	DAB	WALL	27	1673 2431
Oct-Dec	NAC						24	334 1328

Station 106 is located at the north end of the westside shoals. As with station 103 to the south, the midwater catch most often consists of northern anchovy and jacksmelt, but here both species are regular only during the period from April to December. From January to March there is no consistently caught species. Commonly occurring here, but not regularly at most other sites, is the walleye surfperch during the months from April to September.

In the otter trawl there is an assemblage of fish similar to that characterizing station 103 but here the group (containing shiner perch, walleye surfperch, English sole and bay goby) persists as a regular feature of the catch into the summer months.

Central Bay
Segment CB3
Station 213

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						11	115 1017
Apr-Jun	PH	NAC	KS				18	2213 29348
Jul-Sep	PH	NAC	JACK				13	4956 27295
Oct-Dec	PH	NAC					12	270 2802

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DAB	NAC	LFS				27	200 238
Apr-Jun	WCRK	NAC	LFS	ENGL	MID	DAB	26	345 610
Jul-Sep	MID	DAB	WCRK	LFS	NAC	SP	32	772 827
Oct-Dec	MID	LFS	NAC				22	462 535

Segment CB3 includes the Golden Gate and the deepest station sampled by the Bay Study is station 213 (24 m). Midwater trawl catch is largely northern anchovy which are common at most stations. Of particular interest is the regular catch of outmigrating chinook salmon smolts during the season from April to June and their absence in the catch from January through March. Species richness in the midwater trawl peaks at this time.

The greater sampling depth of the otter trawl is reflected in the much smaller catch of anchovy, which is not as regularly caught as other species in all seasons. The more regular occurrence of longfin smelt in the otter trawl than in the midwater trawl seems noteworthy. Plainfin midshipmen are most often caught from April to December while speckled sanddabs are caught most regularly from January to September. White croaker, English sole and shiner perch contribute to greater predictability of the otter trawl catch in the months from April to September. Species richness in the otter remains high through the year.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	LFS	JACK				19	621 2109
Apr-Jun	PH	NAC	JACK	WCRK	KS		20	3655 17370
Jul-Sep	NAC	PH	JACK				19	3362 33005
Oct-Dec	NAC	PH					13	187 10731

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL	WCRK	DAB	STAG	LFS	31	2270 2368
Apr-Jun	ENGL	STAG	DAB	WCRK	NAC	SP	29	2186 3742
Jul-Sep	WCRK	BAY	STAG	NAC	ENGL	SP	29	5296 5480
Oct-Dec	WCRK	SP	NAC	ENGL	LFS	DAB	25	2994 3106

The deep channel running north-south between Alcatraz and the Berkeley mudflats is the second deepest station in Central Bay (16 m). The midwater catch shows the same domination by herring and anchovy as at station 213 on the west side of Alcatraz, although northern anchovy are slightly less regular from January to March. Chinook salmon smolts regularly pass through between April and June and are absent from January to March. Jacksmelt are regular features of the catch for most of the year.

The otter trawl samples a high density, species rich and very predictable fish assemblage. Shiner perch, English sole and white croaker are regular inhabitants year round. Speckled sanddabs are common in the three seasons from October to June and staghorn sculpins are regularly caught in the three seasons from January to September. Longfin smelt occur in catches from October to March, and are regular in the midwater trawl in the period when anchovy are least common.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	NAC	JACK				15	302 398
Apr-Jun	NAC	PH	LFS				19	1400 16895
Jul-Sep	NAC	PH	LFS	JACK	SP		20	2155 42079
Oct-Dec	NAC	PH					15	159 17717

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL	STAG	LFS	WCRK	DAB	32	2811 2853
Apr-Jun	DAB	WCRK	ENGL	NAC	LFS	BAY	29	1863 1930
Jul-Sep	ENGL	STAG	LFS	WCRK	MID	SP	31	4368 4461
Oct-Dec	SP	WCRK	LFS	ENGL	MID	BROK	24	1445 1509

The second station in segment CB2 is closer to San Pablo Bay which is reflected in the increasing regularity of longfin smelt in the catch, even outnumbering northern anchovy during the seasonal low in anchovy abundance. Otherwise the midwater samples are quite similar to those of station 214. Chinook salmon were taken in seven of the 27 trawls performed from April to June but in none of the preceding season.

The otter trawl fish catch is also very similar at the two stations, however longfin smelt are caught year-round with English sole and white croaker. Shiner perch is a slightly less regular feature of the catch. Plainfin midshipmen enter the catch from July through December, whereas speckled sanddabs are regular only from January through June. At both stations number of species is high year-round, particularly in January-March, and numbers of fish is high year-round with a peak from July through September.

Segment CB11
Station 216

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	PH	NAC				17	736 1372
Apr-Jun	NAC	PH	LFS	WCRK	KS	JACK	23	4825 19327
Jul-Sep	NAC	PH	SP	LFS	JACK	WCRK	20	2420 36225
Oct-Dec	NAC	PH					17	677 16756

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	STAG	SP	NAC	DAB	ENGL	26	632 673
Apr-Jun	LFS	ENGL	WCRK	DAB	NAC	STAG	27	1327 1416
Jul-Sep	STAG	LFS	NAC	DAB	SP	MID	26	651 747
Oct-Dec	LFS	NAC	ENGL	SP			24	1318 1736

Station 216 is in segment CB11, the northern channel of Central Bay leading into San Pablo Bay. The catch is very similar to that of station 215 but the increasing shallowness contributes to greater similarity between the midwater and otter trawls. The regular catch of white croaker from April to June is probably due to this shallower depth. Chinook salmon again enter the catch regularly in the months from April to June but are absent January to March.

The otter trawl catch is somewhat less abundant and diverse than in the southern stations. Aside from anchovies, only longfin smelt and English sole are commonly caught year-round. Shiner perch are again less dependably present in the spring.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						23	398 420
Apr-Jun	PH	NAC	SP	KS	WCRK		22	2976 33836
Jul-Sep	NAC	PH					21	4625 55567
Oct-Dec	NAC	PH	JACK	WCRK			21	349 8927

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	DAB	ENGL	LFS	NAC	WCRK	28	2572 2808
Apr-Jun	WCRK	ENGL	DAB	SP	LFS	NAC	28	2183 2256
Jul-Sep	WCRK	NAC	SP	LFS	ENGL	DAB	26	3152 3326
Oct-Dec	NAC	ENGL	SP	STAG			20	1024 2497

Segment CB7 contains the shallower areas near the Berkeley waterfront. Northern anchovy and, to a lesser extent, Pacific herring are the most abundant and regular feature of the trawl. Chinook salmon are present regularly from April to June and absent in earlier months.

In the otter trawl the same six species make up the regular catch from January to September: northern anchovy, shiner perch, English sole, longfin smelt, speckled sanddab, and white croaker. Species richness and abundance are also high through these months. During October to December the total catch and the number of species declines and sanddabs, croaker and smelt are unpredictable. At this time, though, staghorn sculpins are regularly captured.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						14	79 124
Apr-Jun	NAC	PH	SP	JACK	WALL		17	1593 31000
Jul-Sep	NAC	JACK	SP	WALL	PH		16	1063 6605
Oct-Dec	NAC	JACK					16	948 1968

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL	SP	DAB	SF		33	663 785
Apr-Jun	SP	BAY	ENGL	NAC	WCRK	SF	25	1745 4236
Jul-Sep	SP	ENGL	NAC	SF	BAY	STAG	24	1557 1918
Oct-Dec	NAC	SP	SF				16	292 1233

Station 212, in segment CB7, is the only shallow (3 m) station in the Central Bay. Jacksmelt is the only species regularly found year-round in the midwater trawl. Shiner perch and walleye surfperch are regular features of the catch from April to September. Species richness is low year-round and abundance sharply declines from January to March. Chinook salmon are seldom collected at this site.

The otter trawl shows a different species assemblage at this site; starry flounder, which are not regularly captured elsewhere in Central Bay, occur regularly year-round at this site with shiner perch and northern anchovy. English sole are less regular from October to December than the rest of the year. Other species are regular for shorter periods of the year than in the nearby channel stations.

San Pablo Bay Channel Station
Segment SP4
Station 325

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	NAC				22	1302 1868
Apr-Jun	NAC	LFS	PH	JACK	KS	WCRK	22	4071 16414
Jul-Sep	NAC	PH	MID	LFS	JACK		15	1449 36882
Oct-Dec	NAC	LFS	SB	PH			18	562 2013

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	YFG	STAG	SB	SP	ENGL	28	1225 1260
Apr-Jun	LFS	NAC	WCRK	STAG	MID	BAY	23	2115 2289
Jul-Sep	LFS	MID	WCRK	NAC	STAG	BAY	23	1749 1834
Oct-Dec	LFS	STAG	MID	WCRK			22	1559 1621

As with Central Bay, the deep station in San Pablo Bay is dominated by the regular appearance of northern anchovies in the midwater trawl in all seasons of the year, with Pacific herring commonly occurring in the catch from April to December. Unlike any of the stations further downstream, though, striped bass are a regular feature of the fish assemblage from October to March. Jacksmelt commonly occur in the months from April to September. Chinook salmon regularly occur in the trawls from April to June.

The fish assemblage from the otter trawl is quite different than at sites downstream; staghorn sculpin is a regular part of the catch year round and longfin smelt is the most frequently encountered species in all seasons of the year. Plainfin midshipmen and white croaker enter the catch for most of the year (April to December) and bay gobies, like jacksmelt in the midwater trawl, are regular parts of the seasons collections.

North side stations

Segment SP3

Station 323

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						12	117 124
Apr-Jun	NAC	PH	JACK	LFS	SP		17	3225 14589
Jul-Sep	NAC	PH	JACK				17	459 15946
Oct-Dec	NAC						15	281 6118

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	YFG	SF	SB	STAG		23	579 590
Apr-Jun	STAG	BAY	NAC	WCRK	LFS	ENGL	23	1892 2422
Jul-Sep	STAG	NAC	BAY	MID	WCRK	SP	21	2763 3016
Oct-Dec	NAC	LFS					22	1014 1183

Northern anchovy is the only regular feature of the midwater trawl catch for all seasons. During the season from April to September Pacific herring and jacksmelt also occur regularly. Generally the catch is depauperate and small except for the large seasonal influx of anchovy.

The otter trawl catch is dominated by the regular catch of longfin smelt and staghorn sculpin for three seasons of the year. Bay goby and white croaker are a regular part of the April-September catch. This is the furthest downstream station where striped bass and yellowfin goby are regularly captured.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						9	194 266
Apr-Jun	NAC	JACK	PH	LFS			15	3052 6470
Jul-Sep	NAC	SP	JACK				17	2209 16405
Oct-Dec	NAC	AMS					11	163 2210

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	STAG				20	704 717
Apr-Jun	BAY	ENGL	STAG	SF	WCRK	NAC	20	2607 2910
Jul-Sep	NAC	SP	STAG	YFG	SF	SB	20	1363 1788
Oct-Dec	NAC	LFS	SF				14	395 846

The midwater trawls at this station, in the middle of the shallow area of San Pablo Bay, is characterized by the increased dominance by longfin smelt and by the seasonal presence of American shad. Jacksmelt and shiner perch are regular features in spring and summer.

The otter trawl catch shows greatest predictability from April to September when several species that are more common in South and Central Bays appear to invade San Pablo Bay, including bay goby, English sole, and white croaker. Starry flounder are the most frequently captured flatfish. Striped bass are more regular here than at station 323 downstream.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						15	218 225
Apr-Jun	NAC	PH	JACK	LFS	SP		15	2350 12177
Jul-Sep	NAC	LFS	JACK	SB	SP		19	1899 21842
Oct-Dec	NAC	LFS	AMS				12	279 2943

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	492 505
Apr-Jun	STAG	LFS	ENGL	NAC	SF	WCRK	20	1941 2272
Jul-Sep	NAC	SF	STAG	YFG	SP	LFS	17	2745 3148
Oct-Dec	NAC	LFS	SB	SF			15	636 1056

Longfin smelt dominate the catch in all seasons in both nets at station 321 and is the only regular feature of the midwater catch from January to March. In the midwater trawl, American shad are a regular feature, as they were at station 322. This is the furthest downstream site where striped bass are a regular feature in the midwater trawl. Jacksmelt and shiner perch regularly enter the catch in the months from April to September.

In the otter trawl, starry flounder are regularly abundant from April to December. Warmer months are accompanied by regular occurrences of several species, while the wetter months support fewer regular species. Striped bass occurs regularly from October through March but is irregularly caught in warmer months.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	SF				14	566 570
Apr-Jun	NAC	LFS	JACK	PH	SB		20	4478 14104
Jul-Sep	NAC	LFS	JACK				14	1531 18965
Oct-Dec	NAC	AMS	SB	LFS			17	514 2915

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SF	SB	STAG			17	565 579
Apr-Jun	LFS	STAG	NAC	SF	ENGL	SB	25	2407 2738
Jul-Sep	NAC	SB	SF	STAG	LFS	SP	18	1421 2692
Oct-Dec	SB						12	347 553

The midwater trawl at the northernmost station in San Pablo Bay reflects the trend in species composition that is displayed in the series of downstream stations. Longfin smelt are regularly caught in all seasons, striped bass are found through most of the year, jacksmelt are present during from April through September and Pacific herring are regular only in spring. The increasing dominance of the otter trawl catch by starry flounder is reflected in the regular catch of starry flounder in the midwater trawl and is explained by the fact that this is the shallowest station in San Pablo Bay (2.6 m).

The otter trawl is regularly characterized by the presence of four species that are less common in the downstream embayments: longfin smelt, striped bass, starry flounder and staghorn sculpin. Species richness is low, but rises in the summer with the regular appearance of species more common downstream: shiner perch, northern anchovy and English sole.

East side stations
Segment SP5
Station 317

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar							21	1336 1343
Apr-Jun	PH	NAC	JACK	SP			24	1474 8694
Jul-Sep	NAC	JACK	PH	SP	WALL		20	1074 20180
Oct-Dec	NAC	JACK					10	188 1292

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL	LFS	SB	STAG	SP	BAY	30	890 897
Apr-Jun	ENGL	STAG	SF	SP	BAY	LFS	33	1606 1676
Jul-Sep	NAC	SP	ENGL	BAY	STAG	SF	23	2716 3468
Oct-Dec	NAC						18	243 450

The midwater catch at station 317 records 21 species and 1343 individuals, but none occurred in more than 8 of the 27 trawls during January to March. The remainder of the year was consistently made up of northern anchovy and jacksmelt, with shiner perch and Pacific herring from April to September. This is the most upstream site where walleye surfperch are regularly caught.

Otter trawl catches show a consistent set of species through the first nine months of the year: English sole, Staghorn sculpin, shiner perch, bay goby. At the start of the water year all these species fall to much less predictable status, species richness drops to about half of that in the January-June, and fish abundance is very low. Striped bass regularly show up in the catch for January to March and longfin smelt arrive and consistently persist through June.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						22	470 490
Apr-Jun	NAC	PH	JACK				21	3459 11981
Jul-Sep	NAC	JACK	SP	PH			19	974 14854
Oct-Dec	NAC	AMS	JACK				12	238 3742

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	YFG	ENGL	SF	LFS	BAY	25	639 665
Apr-Jun	STAG	BAY	ENGL	WCRK	SP	LFS	23	1537 1647
Jul-Sep	NAC	SP	SF	STAG	SB	LFS	22	2714 3330
Oct-Dec	NAC						16	361 599

As in the shallow stations on the north side of San Pablo Bay, American shad are a regular feature of the midwater catch at Station 318 from October to December. As at the shallow stations on the other side, jacksmelt and Pacific herring regularly enter the catch starting in the April but here jacksmelt stay into the October-December season.

The fishes of the otter trawl are regular in their occurrence at this station but there is less consistency across seasons, most are present consistently for only one or two species, only longfin smelt are regular across three seasons. As at the other stations, the start of the water year coincides with a sharp decline in number of species, number of fish and consistency of catch across years.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	286 382
Apr-Jun	NAC	PH	JACK				15	1126 10892
Jul-Sep	NAC	JACK	SB				13	677 18634
Oct-Dec	AMS	NAC					12	152 776

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS	YFG	ENGL	STAG	26	1484 1514
Apr-Jun	STAG	ENGL	NAC	SF	SP	LFS	21	3330 3472
Jul-Sep	SF	SB	NAC	SP	LFS	STAG	21	3681 3904
Oct-Dec	SB						12	328 345

The third station on the shallows of the east side of San Pablo Bay (319) is very similar to station 320 at the uppermost range of shallows on the other side of the channel.

Like 320, 319 regularly catches American shad and striped bass in the midwater trawl, with jacksmelt entering the catch from April to September, and with Pacific herring regularly occurring in only one season. Unlike 320, the midwater trawl only regularly catches longfin smelt from January through March, instead of year-round.

The otter trawl catch is very similar on the two sides of the channel. The same set of four species is present in three seasons: longfin smelt, starry flounder, striped bass, and staghorn sculpin. Northern anchovy and shiner perch again enter the catch primarily during the months from April to September. Finally, the number of species, number of fish, and number of consistently captured species all fall drastically in the season from October to December, leaving striped bass as the only dependable part of the catch.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	1346 1371
Apr-Jun	LFS	NAC	SB				18	1009 3397
Jul-Sep	NAC	SB	LFS	MID	PH		16	753 20361
Oct-Dec	LFS	SB	NAC				15	2612 3628

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	STAG				19	367 374
Apr-Jun	LFS	NAC	STAG				17	340 395
Jul-Sep	LFS	NAC	SB	STAG	MID	YFG	14	611 733
Oct-Dec	SB	LFS	STAG				11	465 478

This station falls within the San Pablo embayment scheme of Gunther (1987) as segment SP7 but the fish fauna is obviously much more like that of Suisun Bay. Longfin smelt and striped bass are regularly found in the trawls of both nets in all seasons (except for the low predictability in catch of striped bass in the otter trawl for the April-June season). Plainfin midshipmen occur in both trawls in the summer months. Northern anchovy are rarely caught in the months from January to March, but are common in other seasons. Staghorn sculpin is the only bottom species caught consistently year-round. None of the flatfish are regularly captured here in any season and yellowfin goby are found in the otter trawl during the months from July to September.

Suisun Bay Channel stations
Segment SU1
Station 428

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					13	1564 1564
Apr-Jun	LFS	NAC	PH	SB			16	1240 3091
Jul-Sep	NAC	SB	LFS				13	1515 4463
Oct-Dec	LFS	SB	NAC	AMS			12	858 2800

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	YFG				16	390 391
Apr-Jun	LFS	STAG	NAC				16	1394 1448
Jul-Sep	STAG	NAC	YFG	LFS	SB		12	801 842
Oct-Dec							13	212 227

Midwater trawls at station 428 consistent include longfin smelt and striped bass in all seasons of the year. Northern anchovy invade from April to September and young American shad pass through from October through December.

Otter trawl catches are much less consistent and in winter there is no species found in more than one third of the trawls performed. In the first nine months of the year longfin smelt are the most regular part of the catch. Species richness is much lower than in downstream sites and number of individuals is about half of that found at the channel station in San Pablo Bay. Northern anchovy seasonally enters the catch, but at very low numbers.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	830 831
Apr-Jun	LFS	SB	PH	NAC			15	895 2788
Jul-Sep	NAC	SB	LFS				14	408 1338
Oct-Dec	SB	LFS	AMS				15	1244 1292

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	STAG	YFG			13	325 325
Apr-Jun	STAG	LFS	YFG	SF	SB		17	657 666
Jul-Sep	SB	STAG	SF	YFG	LFS		17	672 689
Oct-Dec	STAG	SB	LFS				11	290 292

Station 432 is close to station 428 and the midwater trawl catches are almost identical, although fish abundance is lower and fewer anchovy are found here.

The otter trawl catch, however, is much more predictable than at station 428. This reflects the fact that this station is at the edge of the shallow stations of Suisun Bay where the fish community is very similar and predictable. Striped bass, longfin smelt, and staghorn sculpin are regularly caught year round and yellowfin goby are regular residents of three seasons. Starry flounder are regular members of the benthic community during summer months.

Midwater Trawl Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	766 768
Apr-Jun	LFS	NAC	SB				13	958 1721
Jul-Sep	SB	NAC	LFS	YFG	DS	AMS	14	2251 4067
Oct-Dec	LFS	SB	NAC				14	1513 2061

Otter Trawl Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	263 263
Apr-Jun	LFS	YFG	SB	STAG			17	866 885
Jul-Sep	SB	STAG	YFG	LFS	NAC	SF	13	795 856
Oct-Dec	LFS						11	565 566

Midwater catch at station 429, at the mouth of Grizzly Bay, usually contain longfin smelt and striped bass in each season. American shad regularly occur at this site between July and September, earlier than they do at downstream sites. This is the most downstream station at which delta smelt occur regularly, in summer.

Otter trawl catches also regularly contain longfin smelt throughout the year; striped bass are found regularly in all seasons except October to December. During summer months starry flounder, yellowfin goby and staghorn sculpin are a regular part of the catch.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					11	329 329
Apr-Jun	LFS	KS	SB	NAC			10	432 712
Jul-Sep	SB	LFS	AMS	NAC	YFG		15	1358 1936
Oct-Dec	SB	LFS	AMS				15	2118 2328

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					12	145 145
Apr-Jun	LFS						15	522 531
Jul-Sep	SB	YFG	LFS	SF			12	455 485
Oct-Dec	LFS						9	499 500

Like the other, downstream, shoal stations of Suisun Bay the midwater catch at station 433 is dominated by longfin smelt and striped bass in all seasons of the year. Northern anchovy invade during the summer. American shad are regularly caught in the period from July to December.

The otter trawl catch is small throughout the year. Longfin smelt are commonly caught in all seasons. Other species common in Suisun Bay are sometimes listed as regularly occurring, but the lack of consistent catch is probably a reflection of small total catches.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	DS				10	162 162
Apr-Jun	SB	PH	LFS	NAC			16	669 1051
Jul-Sep	SB	NAC	LFS	ST	AMS	YFG	18	3517 4264
Oct-Dec	LFS	AMS					14	1242 1727

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS	YFG			15	430 430
Apr-Jun	SB	YFG	LFS	STAG	SF		15	1192 1197
Jul-Sep	SB	YFG	STAG	SF	LFS	NAC	14	1789 1823
Oct-Dec	SB	LFS	YFG	STAG	SF		12	726 732

Station 430 is near the mouths of Suisun and Montezuma Sloughs. Thus, the station receives water out of Suisun Marsh and the Sacramento River. The station shows high consistency in the catch of both nets within a context of low species diversity. Like the midwater trawls of the channel stations, longfin smelt are present year round and striped bass are caught regularly in most of the year except October-December. American shad appear in the trawls from July to September. Delta smelt is regularly caught in January to March and splittail are regularly caught from July to September; these species appear to be characteristic of shallower habitats, with splittail maintaining a large part of its population in the shallow sloughs of Suisun Marsh.

The midwater trawl largely consists of repeated captures of a core of five species: striped bass, yellowfin goby, longfin smelt, starry flounder, and (in three seasons) staghorn sculpin. This consistency is particularly remarkable because these species comprise a third of the total number of species that have ever been caught here.

Station 431

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DS	LFS	SB				13	250 250
Apr-Jun	SB	NAC	PH	LFS			14	388 753
Jul-Sep	SB	NAC	LFS	AMS	DS	ST	13	973 1698
Oct-Dec	LFS	SB	AMS	DS	NAC		13	1392 1503

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS				16	408 408
Apr-Jun	SB	SF	LFS	YFG	STAG	ST	18	627 639
Jul-Sep	SB	SF	YFG	LFS	STAG	NAC	16	3491 3523
Oct-Dec	SB	LFS	YFG	STAG	SF		10	731 737

Station 431 is on the south side of Grizzly Bay, opposite station 430 . Midwater trawl catch is almost identical at the two stations except that delta smelt is caught July through January which doubtless reflects the fact that adult delta smelt have moved out to spawn and die and that the young are too small to be collected in the trawl. The regular occurrences of anchovy, American shad and splittail are identical to those at station 430.

Otter trawl catches are also very similar at the two stations, with a set of five species dominating all aspects of the catch. Striped bass, starry flounder, longfin smelt are found in all four seasons while yellowfin goby and staghorn sculpin are regularly present from April through December. The absence of delta smelt from the otter trawl while they are present in the midwater trawl at this shallow station (3 m) emphasizes the presumed surface orientation of this fish.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	DS					13	184 184
Apr-Jun							13	133 248
Jul-Sep	SB	NAC	AMS	LFS	WS	DS	16	2931 3083
Oct-Dec	LFS	SB	AMS	DS			12	690 913

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF					12	224 224
Apr-Jun	SB	SF	YFG				14	723 724
Jul-Sep	SB	YFG	LFS	SF	ST		16	4126 4130
Oct-Dec	SB	LFS					14	915 915

Station 534 in Honker Bay is very different than the similar shoal stations in Grizzly Bay. The midwater trawl shows extremely low catches from April to June, with no species being caught consistently. Longfin smelt and delta smelt are the most regular part of the catch. At other stations in Suisun Bay, American shad are present regularly from July through December. Uniquely, white sturgeon are caught regularly at this station; these are not young of year as is the case for several other seasonal catches (sizes range from 304 to 671 mm SL).

Otter trawl catch is dominated by striped bass in all seasons and starry flounder for all periods except October-December. Longfin smelt are regular only in summer months. The seasonal catch of splittail is one point of similarity with the catch in Grizzly Bay.

Western Delta
below confluence of Sacramento and San Joaquin
Station 535

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					11	248 248
Apr-Jun	KS	LFS	SB				13	254 331
Jul-Sep	SB	LFS	AMS	DS	YFG	NAC	15	2931 3083
Oct-Dec	LFS	SB	AMS				12	613 670

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						14	147 147
Apr-Jun	LFS						17	367 369
Jul-Sep	SB	LFS	YFG				12	847 851
Oct-Dec	LFS	SB					15	366 382

Catch at this station is very similar to the channel stations downstream in Suisun Bay. Longfin smelt and striped bass are found year-round. American shad enter and pass through from July to December, chinook salmon smolts pass through from April to June and northern anchovies enter in the summer. Delta smelt are a regular member of the midwater catch in July through September as they are downstream at station 429.

Like the other deep channel stations above Carquinez Straits, the otter trawl catch is not very predictable; longfin smelt occur year round and striped bass are regularly caught from July through December.

Sacramento River channel
Station 736

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					14	202 202
Apr-Jun	KS	SB					12	179 180
Jul-Sep	SB	AMS	DS				13	1734 1759
Oct-Dec	LFS	SB	DS				11	386 397

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					12	94 94
Apr-Jun	WCAT						15	279 279
Jul-Sep	SB	WCAT	YFG				13	656 656
Oct-Dec	SB	LFS					13	287 287

Midwater catches at the lower Sacramento River site show the effect of location on seasonality of catch in three migratory species. Chinook salmon and American shad are collected here only in the season prior to their capture at downstream sites. Delta smelt are caught from July on December, probably reflecting their upstream spawning migration from the downstream sites where they are generally collected in the first three seasons of the year. Longfin smelt are collected in both nets only from October to March, which encompasses their likely time of upstream migration from their usual habitat in Suisun and San Pablo Bays. Only striped bass are regularly caught at this site year-round.

The otter trawl catch is very depauperate and catches are very small but this station is unique in that white catfish is a regular element from April through September.

San Joaquin River (shallow channel station)
Station 837

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DS						6	111 111
Apr-Jun	KS						8	106 106
Jul-Sep	AMS	SB					8	1237 1237
Oct-Dec	AMS	SB	TFS				9	346 346

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LOGP					13	261 261
Apr-Jun	SB	SF					13	350 350
Jul-Sep	SB						12	670 670
Oct-Dec	SB						12	363 363

In the San Joaquin River catches in both nets are very low and few species are consistent in their occurrence (which may just reflect the extremely low numbers).

The midwater net displays lower species richness than at any other station in the estuary. This station is also unique in that no anchovies have ever been captured here. Longfin smelt are also a very rare species at this station, making it different than any other station above Point Richmond. The other migratory species found in the Sacramento River similarly pass through this site, but at lower densities. Unique to this site is the presence of threadfin shad at the start of the wet season. As discussed in the section on threadfin shad, this is not an actual migration, but rather a simple washout which carries the shad into cooler waters downstream, with a subsequent winter die-off.

The otter trawl catches striped bass year-round but is distinguished in January to March by the regular presence of bigscale logperch.